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HOST PLANT LOCATION BY LARVAE OF THE WHEAT BULB FLY (*LEPTOHYLEMYIA COARCTATA* FALLÉN)

By D. B. Long

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Introduction

The eggs of the Wheat Bulb Fly are laid most freely in the surface layer of bare soil in summer, and hatch as maggots about 2 mm. long early the next spring, when they will attack young plants of Winter Wheat by boring into the bases of stems, the so-called bulbs, and feeding on the terminal shoots and developing leaves. Further details of the biology of the Wheat Bulb Fly are given by Rostrup (1924), Gemill (1927), Gough (1946), Dobson *et al.* (1958) and Long (1958*a*, *b*, *c*).

During the egg stage the soil will usually have been ploughed so that the eggs may be buried to depths of up to 10 or more inches ; Gough (1946) found that larvae from eggs buried 18 inches were still able to infest wheat plants growing on the surface. This raises the problem of the mechanism of plant location. By what route does the larva travel from the egg to the plant ? Is plant location purely a matter of chance or do the plant roots guide the larva, or is there some other mechanism ? Naturally these questions are of interest in planning methods of control such as the positioning of insecticides. Whilst the known range of host plants includes certain cereals and wild perennial grasses (Gough, 1946 ; Stokes, 1955), the experiments about to be described were restricted to Winter Wheat *var.* Cappelle.

Pot Experiments

To investigate these problems a series of experiments was designed in which different regions of wheat plants were exposed to the larvae, the remainder of the plants being confined within glass tubes. In the first series only the roots at a distance from the plant base were exposed, in the second the whole root system, and in the third the stems only. A relatively small physical margin existed for the separation of stem and root exposures, whilst the possibility existed of larval movements becoming more erratic with time and so producing an anomalous result due to the experiment itself. Accordingly, as the intention was to ascertain the normal route of approach, the root and stem regions were presented in the form of a choice experiment.

The experiment was begun in mid-December, using standard 11-inch earthenware flower pots in which 24 glass tubes of $\frac{3}{4}$-inch diameter were set vertically in two concentric rings, with 8 tubes in the inner ring and 16 in the outer. These were so arranged that the distance between adjacent tubes in both rings was the same and so that those in the inner and outer rings did not fall on the same radii (fig. 1). An additional tube of $\frac{1}{4}$-inch diameter and 6 inches long was put centrally in each pot so that the lower open end lay 5 inches below the soil surface. In setting up the pots the positions of these tubes were ensured by the use of wire spacers. In the ten pots of series A, tubes 3½ inches long were set so that the tops were ¾ inch above soil level. These were individually filled with sifted soil, a germinated seed being introduced in the process so that it lay 1 inch below the soil surface; the pots outside the tubes were filled to the same level with soil. For series B (20 pots), tubes 7½ inches long were set in alternate positions in the spacers so that the tops were 1½ inches below the top of the pots which were filled with soil outside the tubes to 2¼ inches below the top. Short tubes (2 inches long) were then put into the remaining positions in the spacers, and both the pots and tubes filled with soil up to 1 inch from the top of the pots, one germinated wheat seed being introduced into each tube so that it lay 1 inch below the soil level (fig. 2). In series C (ten pots), which served as a control, 24 germinated seeds were set in the appropriate positions, 1 inch below the soil level without the introduction of glass tubes.

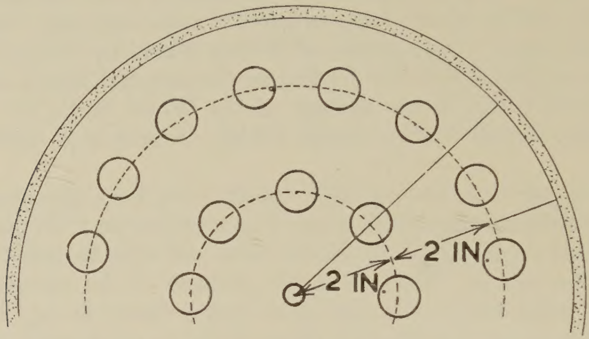

FIG. 1.—Plan of tube layout in pot experiments.

Before use the soil was passed through a ½-inch mesh screen, and to minimise subsequent soil movements it was progressively firmed throughout the process of setting up the pots. In order to avoid the introduction of naturally occurring eggs, the soil for these experiments was taken after the removal of the top 3 inches from an area which had not been disturbed throughout the egg-laying period in the previous summer.

The open upper ends of the central tubes were covered with inverted, closely fitting specimen tubes to prevent the entry of water or other extraneous matter. The projecting edges of the other tubes were smeared with grease-banding compound to prevent larvae reaching the plants by this route. Whilst the plants were growing the pots were stored in an open-sided insectary and watered sufficiently to ensure that the soil was kept uniformly damp throughout the pots.

Each pot was inoculated on 27th February, 1957 with 20 freshly hatched larvae. This was carried out by pulling up the central tubes 1 inch and then inserting a fine pipette 6½ inches long containing 20 larvae in 1 to 2 ml. of water so that they were ejected below the level of the lower open end. The tubes were raised a further inch and the lower ends rinsed down with a little more water before replacing the covers.

The inner and outer rings of plants were sampled separately three weeks later on 20th March and the results are summarised in Table I. Plants in which the roots or stem had not remained confined to the tubes as planned were discarded.

As the number of larvae which could be expected to infest the plants in

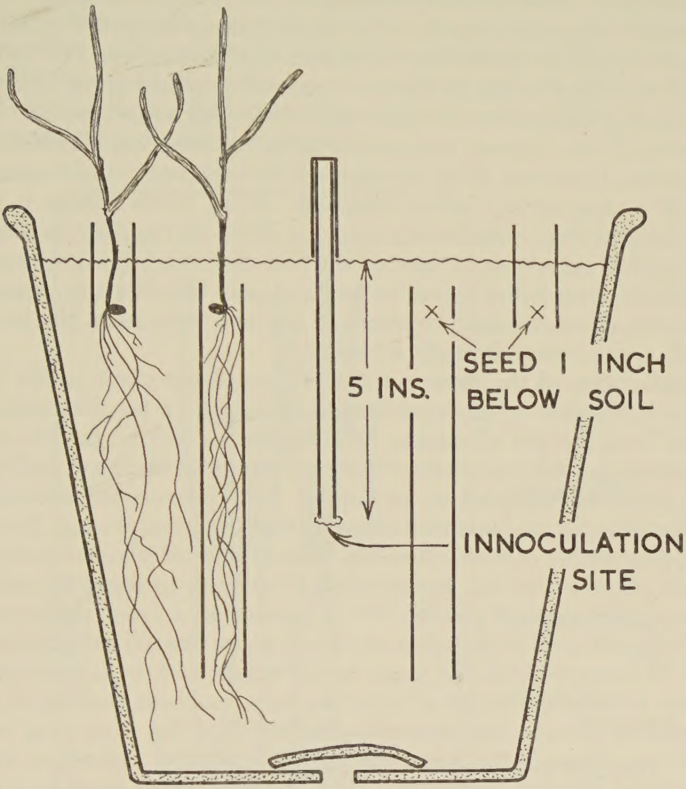

Fig. 2.—Section of pot showing arrangement for exposing the entire root or the stem in the choice experiment.

Table I.—*Effect of region of plant exposure on the infestation of wheat plants following an inoculation with* 200 *freshly hatched larvae per treatment*

Exposed region of plant	Plant ring	Number of plants	Number of stems	Number of damaged stems	Number of recovered larvae	Mean larval wt. (mg.)	Mean instar	Mean number larvae/plant
A. Root–"extremities"	Inner	80	84	6	6	1·90	2·8	0·075
	Outer	160	171	4	4	1·43	2·3	0·025
B_1 Root—entire .	Inner	80	82	11	13	1·51	2·2	0·163
	Outer	159	170	18	18	1·43	2·1	0·113
B_2 Stem . .	Inner	79	84	41	43	1·41	2·3	0·544
	Outer	157	173	88	94	1·44	2·3	0·599
C. Stem and root	Inner	80	102	34	33	1·62	2·6	0·425
	Outer	160	192	55	52	1·23	2·2	0·325

series A by chance was 27, and the number observed (10) was appreciably less than this, the results strongly suggest that roots $1\frac{3}{4}$ inches or more from the plant served little or no function in the location of the plant by the larva. In series B, however, where virtually the entire root system was exposed, assuming that the other tubes exposing the stem region played no part beyond reducing the available space for the larvae, the chance expectation was 14. As this value was clearly exceeded in the 31 larvae recovered, it would appear that the root zone less than $1\frac{3}{4}$ inches from the plant base could play an active part. When the stem in series B was exposed the number of larvae observed increased fourfold, whilst less than 1 per cent. of the larvae could be expected to have made a chance location of a stem of 0·1 inches diameter. From these results it is readily apparent that the stem constitutes a principal factor in the plant location, which is not altogether surprising in view of the fact that the larva burrows into the stem whilst the roots never appear to be damaged. Occasionally, when present, the sub-crown internode may be attacked but this only leads the larva to the wheat bulb above, where it finally settles.

A consideration of the mean number of larvae per plant in the inner and outer rings in relation to the tube situations suggests a possible path of larval movement from the site of release. If infestation occurred in the course of a purely random upward movement, the mean values for the inner and outer rings of plants could be expected to be similar, but observations showed that, in general, the mean for the inner ring exceeded that of the outer ring. Furthermore, in series A the number of larvae observed fell well short of the chance expectation. This would suggest that the larvae tend to move up towards the surface at a fairly steep mean angle of possibly 60° or greater, as a lower value would have brought the lower ends of the tubes of series A more directly into the mean path. Also, if it be accepted that the mean larval weight and, to a lesser extent, the mean instar reflects the length of time the larva has been feeding in the plant, it is interesting to note that generally the larvae in the inner ring were more developed than those in the outer and therefore support the above suggestion. The exceptions appear in series B_2. Here the long tubes came up to within $\frac{1}{2}$ inch of the surface, and the infestation of the outer ring was slightly the more successful, which suggests that the angle of larval movement was not sufficiently great to bring them to the surface inside the inner ring, whilst supporting the earlier postulate of about 60° in that the larvae would then have surfaced nearer the outer ring than the inner.

The experiments of Stokes (1956) showed that plant exudates could be a prime factor in the mechanism of plant location. From the above experiments it appears that the stem plays the major part, whilst the root zone close to the plant base may also be involved, but it cannot be determined from this set of experiments whether the apparent attractiveness of the root zone was due to a local root exudate or to stem exudate which had either diffused or been washed down the tube when the pots were watered. Accordingly a further series of experiments were carried out in the laboratory to clarify this point.

LABORATORY EXPERIMENTS

The technique used to study the effects of possible root and stem exudates was based on that described by Stokes (1956). In order to determine if the soil in the root zone was, in fact, attractive to the larvae apart from any guiding function the roots might serve, and that the effects observed in the pots was not an anomaly due to the tubes, five samples each consisting of ten young undamaged wheat seedlings were dug up and the soil surrounding the stem, bulb and seed case was carefully removed. The soil surrounding the roots was washed off in 50 ml. of distilled water and, when thoroughly broken down, was filtered through a fine grade filter paper and the filtrate made up to 50 ml. with further washings. With the filtrate a jelly was made up with sodium alginate "Manucol" SS/LH 0·7 g. and calcium citrate 0·13 g. and then cut into ¼-inch cubes. Similar control jelly was made up with distilled water.

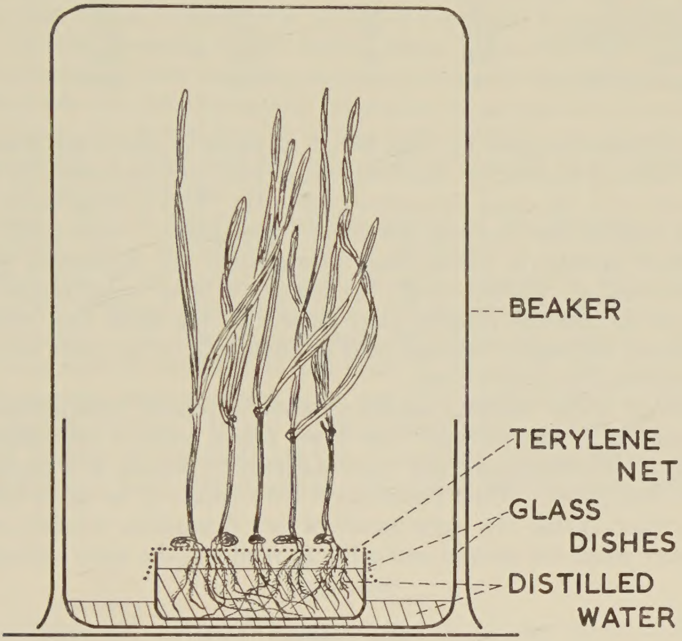

Fig. 3.—Method for obtaining the root exudates used in experiments.

A cube of the experimental jelly and another of the control were set up ¾ inch apart on damp black filter paper in a petri dish, and freshly hatched larvae were released centrally between the two cubes. The petri dish was then closed and kept in the dark between observations made at 15 minute intervals. The experiments were carried out between 19° and 23° C., and the temperature did not vary more than 2° within the course of any one experiment, which would last from 60 to 90 minutes.

The results, which are given in Table II, show that root soil was attractive, even at the dilution associated with the soil washing, in having nearly one quarter of the larvae in it. However, since the possibility still existed that, as in the pot experiments, the soil may have been affected by exudates from the stem, a further series was set up to study the isolated root.

Germinated wheat seeds were placed on terylene mesh stretched over the petri dishes so that their roots dipped into water in the dishes (fig. 3). When the seedlings were well developed the root waters in the petri dishes were used to make up jellies, which were tested as previously. The results given in Table II show that the root itself produced an attractive substance.

Table II.—*Larval response to jellies made with various solutions*

Jelly solution	Number of larvae observed in jelly		Larvae wandering	Total larval observations	% larvae in experiment jelly
	Experiment	Control			
Root soil extract .	60	15	185	260	23·1
Root culture solution .	110	19	217	346	31·8
Plant water . .	130	20	192	342	38·3
Guttation droplets .	64	16	195	275	23·3

When jellies were made up from 50 ml. of water in which ten washed seedlings were allowed to stand so that their stems were well immersed for 48 hours, they proved to be the most attractive (Table II). This is even more apparent when it is realised that the less attractive " root jellies " were made after ten or more days growth in which time, presumably, the attractant substances were concentrating. Unfortunately the results of these experiments were not quantitative, so that the relative part played by the roots and stem cannot be determined, although it appears that in the course of two days the stem can make an appreciable contribution.

The young wheat seedling exudes guttation droplets from stomata in the leaf tips and, as it was thought that these might prove a convenient source of the attractive substances, they were collected by means of a capillary tube and made into jellies. When tested they were found to be attractive but to no great extent (Table II). As a result of dew formation, rainfall, etc., these droplets may reach the ground and serve to reinforce the stem exudate.

Discussion

The success of larval infestation must depend to some extent on the possible length of life of the newly hatched larva without plant food. In the laboratory at room temperature where the temperature never fell below 15° C. and occasionally exceeded 20° C. (at the time the pot experiments were started) 50 per cent. of the larvae have been found to survive for 12 days, so that at outside temperatures the duration may have exceeded this. Whilst the rate of larval movement is not known, the larvae in the pots had a minimum distance of 6½ inches to cover to reach the outer ring of plants, and, from the results of these and other experiments, it would appear that distance was not a limiting factor in the larval route.

The experiments both in the pots and the petri dishes support the suggestion of Stokes (1956) that plant exudates form a prime factor in the plant location mechanism. It has been shown that the roots close to the wheat bulb can play a part in both sets of experiments, whilst the stem appears to play the major role. It is nonetheless remarkable that a larva a little more than 2 mm. long, moving through such a heterogenous medium as soil, can make a response which gives the appearance of being directional and is certainly adequate for plant location.

Naturally there will be a certain mortality in the process of infestation which, in the case of the pots, amounted to over half of the larvae introduced in the control series. In this respect it is interesting to note that the mean number of larvae per plant for stem exposures exceeded that for the whole plant controls (Table II). However, if the results for the roots (B_1) and the stems (B_2) (as equivalent to the entire plant) be summed, there were 168 larvae in 475 plants; that is, a mean of 0·354 larvae per plant, whilst in the controls there were 85 larvae in 240 plants, which also gives a mean of 0·354 larvae per plant, indicating that the experiment was probably successful in separating the root and stem factors operating in the control series. Thus the fact that a higher infestation occurred when only the stems were exposed suggests that the exposure of the roots can actually impede infestation to an appreciable extent. This could be due to the attractiveness of the roots masking the directional effect of stem exudates, in which case the roots may be actually more attractive than indicated by the tube results.

At present little is known about the nature of the attractant present in these exudates, nor is it known if a single substance or a combination of substances are involved. It is evident that the active material is water soluble but direct tests for proteins, amino-acids and carbohydrates have proved negative, possibly because of the low concentration of substances present. It must be expected that work in this direction is likely to be lengthy for, apart from the factors of analysis, testing at each stage can only be effected by a ready supply of freshly hatched larvae. In the course of work so far carried out it has been noted that boiling the solutions kept at a constant volume before making up the jellies reduced their attractiveness. This work is being continued.

SUMMARY

The mechanism of host plant location by newly hatched larvae of the Wheat Bulb Fly has been studied by inoculating pots of prepared young wheat plants and by direct observations of movement in petri dishes.

The results of pot experiments suggest that the larvae move upwards at a fairly steep angle from the egg site and then horizontally in the surface layers of soil. Plant location did not appear to occur as the result of random movements but involved a larval response to attractant material exuding from the plant. The root extremities were not involved in this process, but when roots close to the base of the plant were exposed to the larvae appreciable infestation of the plants occurred. The highest level of infestation occurred in plants in which the stems only were exposed, indicating that the stems played the major role in the location mechanism and that the attractive root zone may actually interfere with infestation.

The attractiveness of the exudates from the root and stem regions was supported by direct observation of larval movements in petri dishes. Leaf tip exudates in the form of guttation droplets were also found to be attractive and may, on reaching the soil, reinforce the stem exudates. The attractiveness of the exudates was reduced by boiling.

ACKNOWLEDGMENTS

I would like to express my appreciation to Mrs. B. Copleston and Miss J. Balshaw for their assistance with the pot experiments and to Miss B. Stokes for her helpful and stimulating discussion of the chemotactic experiments.

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NOTES ON THE BIOLOGY OF A NEW SUBSPECIES OF *ANOPHELES WELLCOMEI* (DIPTERA : CULICIDAE) FROM EAST AFRICA, AND ON THE DISTRIBUTION OF RELATED FORMS.[1]

By M. T. GILLIES

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Anopheles wellcomei erepens subsp. n. (Figs. 1, 3, 5–8)

Female.—Differs from the typical form by the following characters :

Palps with a varying degree of pale scaling (in addition to the main pale bands), this being never very marked and frequently absent altogether. Proboscis with inconspicuous pale scaling, sometimes almost entirely absent. Pharynx with filaments of cones normally fimbriated, post-pharyngeal processes short. Mesonotum scantily clothed on anterior third with narrow golden scales, these being absent from the posterior two-thirds. Wing field predominantly dark scaled except for third, and stem of fifth veins ; pale fringe spots entirely absent posterior to third vein. Legs with pale rings absent, or at most consisting of a few pale scales on the apices of the fore tarsal segments only.

Male.—Shaft of palps with scattered pale scales, these being more numerous on third segment. Genitalia : outer accessory hair of harpago stout and a little longer than club, inner accessory hair normally absent (on 1 harpago out of 5 pairs examined a single fine inner accessory hair was present).

Pupa and larva.—Not separable from the type form.

Egg.—Floats separated by a space equal to their own width, frill narrow, continuous between the floats, and separated to expose a single narrow deck. Fusion of the frill across the mid-line has not been seen. Total length of egg 1·3–1·5 times length of floats (1·7 in typical form (Lewis, 1939)) ; usually 17–19 float chambers, occasionally 16 or 20. Chorion marked with uniform fine stippling.

Holotype female TANGANYIKA : South Pare District, Kihurio, 1.vii.1953. (In the British Museum, Natural History). Paratypes, TANGANYIKA : the Mkomazi valley from Gonja to Mkomazi ; KENYA : Taveta, (*Dr. A. Smith*).

This subspecies differs strikingly from *A. wellcomei wellcomei* by the very dark wings with absence of pale fringe spots behind the third vein and by the almost complete absence of pale markings on the legs. Other differences that may be noted are the distribution of the mesonotal scales, the male genitalia and the relatively greater length of the floats in the egg. There is considerable variation in the amount of pale scaling on the palps, although this never approaches the completely pale outer half of the palps seen in the typical form. The wing markings, however, are very constant. The palmate hairs of the larvae are broader and with more notches on the shoulders than as depicted by De Meillon (1947) in *A. distinctus* Newstead and Carter and *A. theileri* Edwards, but some specimens of *A. wellcomei wellcomei* from Fashoda in the Sudan, kindly lent by Dr. D. J. Lewis, have similar hairs.

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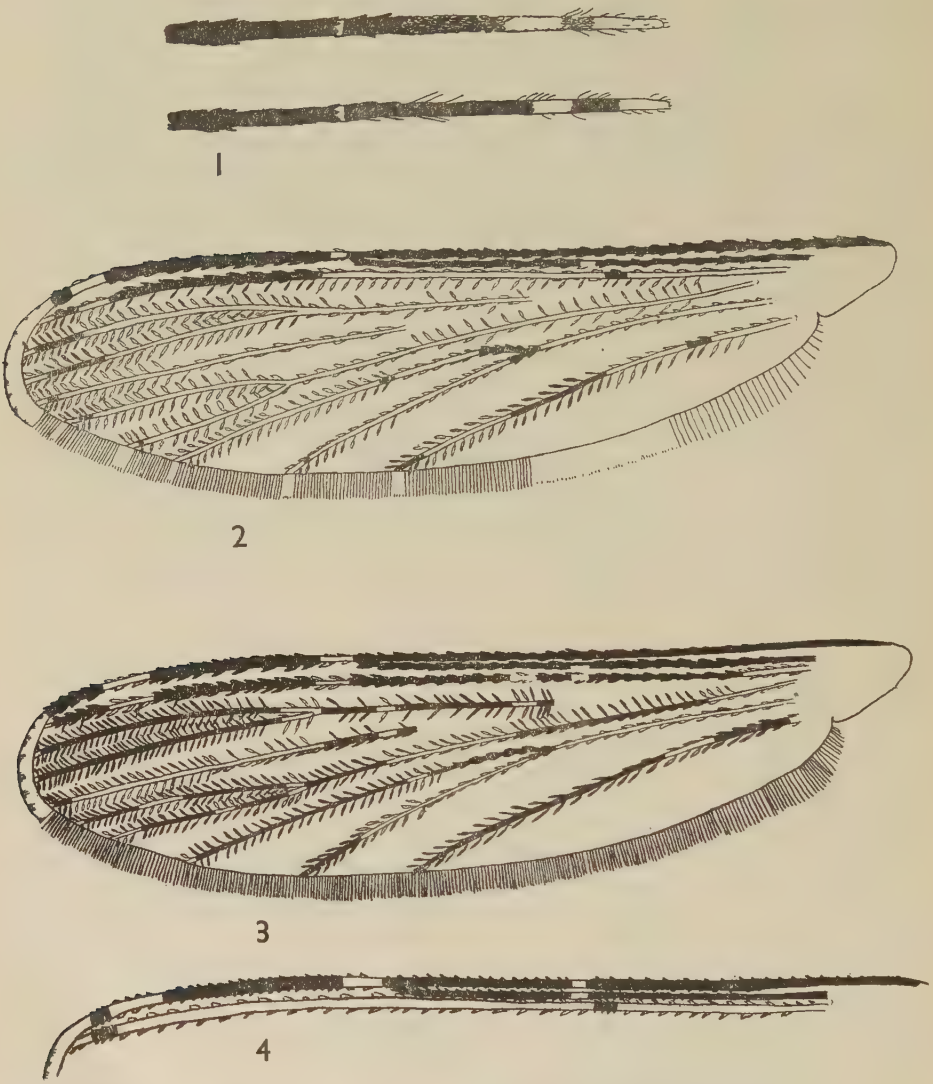
[1] This work was carried out under the administration of the E.A. High Commission with funds provided by the East African Governments, and by the Colonial Office from the research allocation of the Colonial Development and Welfare Acts on the recommendation of the Colonial Medical Research Committee.

Anopheles wellcomei wellcomei Theobald, 1904

Recent records.—Lake Victoria: Ukara Island (Smith, 1955); Uganda: Butiaba (in the collection of the Insect Borne Diseases Division, Nairobi); French Cameroons: Ntem River (Languillon *et al.*, 1956) and Maroua (J. Mouchet, *personal communication*); Northern Nigeria: Mokwa (Dr. L. J. Bruce-Chwatt, *personal communication*); Ethiopia: R. Baro and R. Pibor (Balfour, 1904).

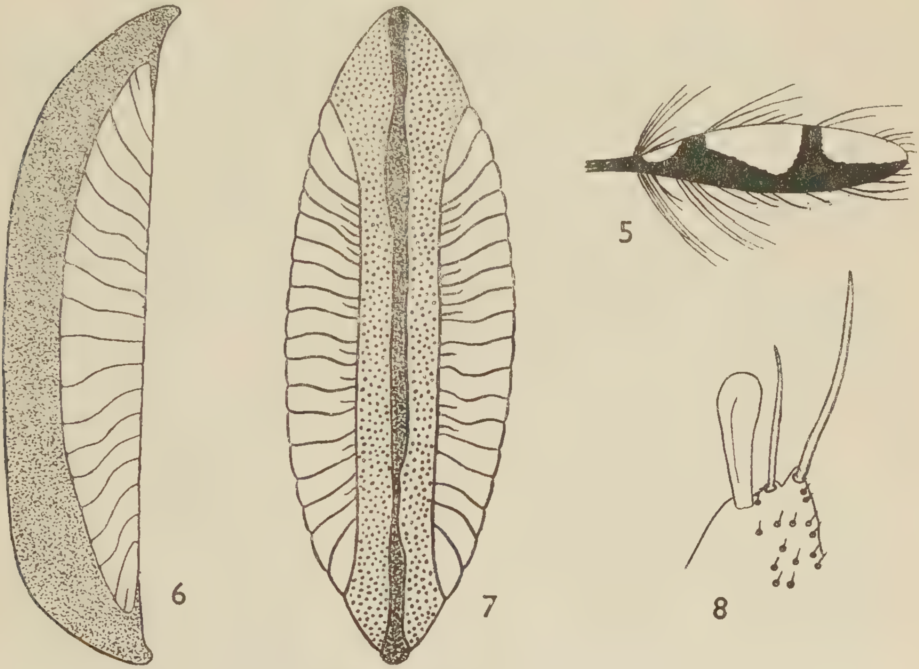


Figs. 1–4.—(1) *A. wellcomei erepens*, female palps. (Two examples to show variation). (2) *A. wellcomei wellcomei*, wing, Ukara Island. (3) *A. wellcomei erepens*, wing. (4) *A. wellcomei*, Zanzibar form, part of wing.

Specimens from Ukara Island, Butiaba, Yaounde in the French Cameroons, and from the Haute Volta have all, on examination, been found to belong to the typical form.

Anopheles wellcomei ugandae (Evans, 1938)

Gillett (1955) described the male of this form and showed that, on genitalic characters, it should be treated as a subspecies of *A. wellcomei* rather than of *A. distinctus*. Both var. *ugandae* and the so-called " dark forms " of *wellcomei* (Evans, 1938) differ only in the amount of pale scaling on the palps and proboscis. Since in *erepens*, as described above, the amount of pale scaling on both appendages is highly variable, and, even in the Sudan, specimens with relatively dark palps occur (Lewis, 1956), it seems to me that both these forms should be regarded as falling within the range of variation of *A. wellcomei wellcomei*.



Figs. 5–8.—*A. wellcomei erepens*. (5) Club of male palp. (6–7) Egg. (8) Harpago.

Anopheles wellcomei subsp. indet

A single female was captured biting man at Kibonde Nzungu, Zanzibar, on 23.v.56. This differs from other forms by the extension of the pale sector spot on to the costa, and by the almost completely pale first vein (fig. 4). The proboscis is entirely dark scaled, but the subapical dark band on the palps is composed of brownish-yellow scales. The rest of the wing field and the legs are as in typical *wellcomei*.

The finding of *A. wellcomei* on the island of Zanzibar extends the known range of the species right across Africa. It is interesting to note that moderately intensive collecting on the adjacent East African coast has failed to reveal this species, although *erepens* is abundant in the more arid regions 100 miles or so inland.

Anopheles distinctus Newstead and Carter, 1911

Recent records.—NYASALAND : Shire River (Berner, 1955). Some larvae from TANGANYIKA : Southern Highlands, Mufindi (*G. R. Webbe*) should probably be referred here.

DISTRIBUTION

Figure 9 shows the recorded distribution of *A. wellcomei* and *A. distinctus.* This map is based on the accounts given by Evans (1938), De Meillon (1947),

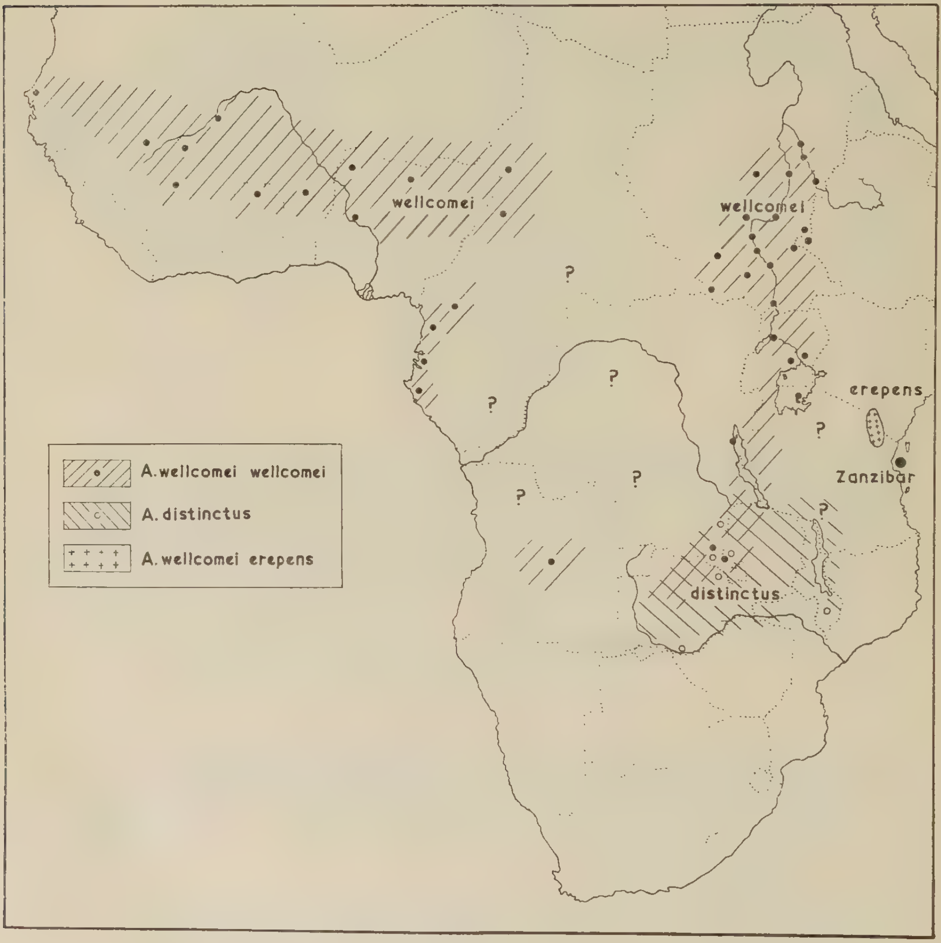


FIG. 9.—The recorded distribution of *A. wellcomei* and *A. distinctus.*

Hamon *et al.* (1956), and on more recent records as cited above. Records for the Sudan are taken from Lewis (1956). The question marks indicate the large areas of equatorial Africa in which the absence of records may partially reflect the absence of collectors. Nevertheless in many parts of West Africa, for instance Nigeria, collecting has been fairly intensive, and it seems likely that *wellcomei* is genuinely absent from much of the West African Subregion as defined by Chapin (1932). It appears to reach its maximum abundance in the dry savannah regions, typical *wellcomei* being common throughout the Sudanese Savannah District, while *erepens* occurs as a group of allopatric populations in the southwards extension of the Somali Arid District in Kenya and Northern Tanganyika. The latter form is particularly common in the rain-shadow area that lies between the Usambara and Pare Mountains of Tanganyika, where the annual rainfall is probably less than 14 inches.

BIOLOGY OF *A. wellcomei erepens*

This insect is most abundant during the months of May to August, following the main rainy season. The larvae have been found in permanent and semi-permanent swamps and streams in the South Pare District of Tanganyika. They show the group habit of climbing up the stems of emergent plants or stakes, thus maintaining themselves a little above the main water surface. They presumably achieve this position by means of the belts of thoracic and abdominal spicules, characteristic of members of the *distinctus-wellcomei* group. It seems that they can maintain themselves in position despite some degree of disturbance of the water surface. If ordinary anopheline larval collecting methods are used, that is to say, if the edge of a bowl is carefully pressed into the water so as to suck the water away from the sides of the breeding site, very few larvae are caught. If, however, the bowl is put in carelessly with a splash, the larvae appear to be dislodged by the bow wave formed and float away into the bowl with the subsequent backwash. Using this method of collecting, it has been noticed that isolated clumps of emergent vegetation are particularly favourable sites for larvae.

The adult mosquitoes have been caught biting man at night on numerous occasions. Biting has been observed more frequently outside than inside houses, although it cannot be claimed that a critical comparison has been made of the two activities. They can, however, be caught most abundantly either biting cattle in the open or resting round thorn animal enclosures at night, and it seems that they are primarily zoophilic. No glands infected with sporozoites were found amongst 127 mosquitoes dissected in South Pare District, It is not impossible, however, that an occasional specimen may live to transmit malaria, as has been shown for *A. wellcomei wellcomei* in the northern Cameroons (Hamon *et al.* 1956). Moreover, Dr. A. Smith has observed *erepens* biting man in large numbers near the Ruvu River in Northern Tanganyika, even after the houses had been sprayed with residual insecticides. In the presence of other more potent vectors it could obviously be of no importance as a malaria carrier, but in localities where it is abundant it should be regarded with suspicion as potentially capable of maintaining low grade transmission out of doors, especially if it should be found that house spraying has failed to eliminate malaria completely.

SUMMARY

A new subspecies of *Anopheles wellcomei*, geographically isolated from other forms of the species, is described from Tanganyika and Kenya. The distribution of this and of other forms is discussed, and notes are given on its behaviour.

ACKNOWLEDGMENTS

I am indebted to Mr. P. F. Mattingly of the British Museum (Natural History) for helpful comments on the taxonomic status of this insect, to Mrs. E. C. C. Van Someren of the Insect Borne Diseases Division, Nairobi, and Monsieur J. Hamon for the loan of material, and to Mr. M. C. F. Butler for the accompanying illustrations.

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THE STYLET MOVEMENTS OF A PLANT-SUCKING BUG, *ONCOPELTUS FASCIATUS* DALL. (HETEROPTERA : LYGAEIDAE)

By P. W. Miles*

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Introduction

Weber (1928), working with *Psylla* nymphs, was the first to make a comprehensive study of the movements of hemipterous stylets in relation to their musculature and to explain the capability of *Psylla* nymphs and of other Homoptera possessing long, thin, looped or coiled stylets to pierce hard materials. The sequence of stylet movements that he proposed, and which has since been repeated unmodified (Weber, 1930, 1933 ; Snodgrass, 1935), is shown in figure 1a.

Weber made his observations on the stylets withdrawn from the labium and held by capillarity under a cover glass, in the insect's own saliva. Although Brocher (1925) had reported that the stylets of *Psylla* nymphs move rapidly back and forth, Weber described only continuous forward movement ; in psyllids, the stylets normally form a loop outside the labium, and the withdrawal of the stylets, shown at the end of the sequence in figure 1a, was due to an attempt by the insect to shorten the loop in the absence of a labial clamp. Zweigelt (1915) believed that aphids controlled the direction taken by their stylets in plant tissue, and Weber assumed the same was true of *Psylla*. He suggested that the maxillary stylets could not move independently at the tips and that, in consequence, if the thrusting forces on them were unequal, the tip of the stylet bundle would curve away from the side that was being pushed harder.

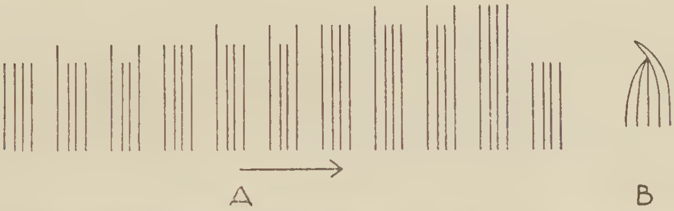

Fig. 1.—(a) Successive stages in the movement of the stylets of *Psylla* nymphs, according to Weber (1928). The outer and inner lines represent the mandibles and maxillae respectively. (b) The tip of the stylet bundle of a *Psylla* nymph, with one mandible advanced, after Weber (1928).

In a later publication, Weber (1930) suggested that the account he had given for *Psylla* nymphs applied to all the Hemiptera, although he thought there might be some difference between phytophagous forms on the one hand and carnivores on the other. He also drew attention to figures in the literature which suggested that the maxillae in some forms could move separately, and he was at a loss to explain how, in such cases, the direction taken by the stylets was controlled.

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EXPERIMENTAL METHODS

The milkweed bug, *Oncopeltus fasciatus* Dall., will feed on agar gels containing sucrose, and if the gel forms a film on a glass slide, the movements of the stylets can be observed under a binocular microscope. Much of the stylet activity observed in this way is too rapid to be appreciated, and, for this study, records were made by cinephotomicrography. As feeding insects were often disturbed when the objective of a monocular microscope was lowered into focus above them, they were made to feed from the " pillory " shown in figure 2. This consisted of a vertical flap rising from a mask of stiff paper which could be fixed with adhesive tape to a slide coated with a suitable substrate. The insect was itself fixed to the mask with adhesive tape, its head placed in a notch in the pillory, and a thin strip of plasticine laid over the top of the thorax to hold the insect in this position ; the rostrum was then eased over the pillory and the tip of the rostrum was thus brought into contact with the substrate. The insect was able to move the tip of the rostrum over the surface of the substrate beyond the pillory and to pierce the substrate with the stylets, to an extent depending on the height of the pillory and the size of the notch holding the head. Generally, the insect would attempt to fold the rostrum back and, although this was prevented by the pillory, the tip of the rostrum would be brought immediately below the pillory where any protraction of the stylets could not be satisfactorily observed. However, if the tip of the rostrum was repeatedly pushed forward along the surface of the substrate by the observer, stylet activity would eventually begin within the substrate some distance in front of the pillory, where the movement could be observed without obstruction.

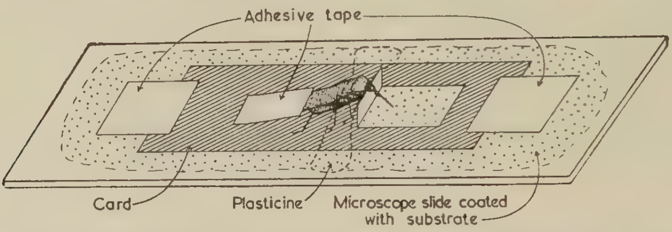

FIG. 2.—Diagram of the feeding pillory used in cinephotomicrography studies of stylet action, with an insect in position.

To obtain photographic records, a substrate containing 3 per cent. agar and 10 per cent. sucrose was used, either immediately on setting (soft medium) or after it had hardened for a day (hard medium). Direct observations were also made on other media such as 5 per cent. homogenised peanut in 3 per cent. agar, saturated sucrose syrup and other mixtures of agar and sucrose.

Oncopeltus feeds naturally on milkweed stems, foliage and seeds and can be reared on a variety of other seeds including peanuts (Frings and Peissner, 1952). It may be objected that, in artificial substrates, behaviour of the stylets may be different from that in the insect's natural food; certainly no observations were made with media as hard as the woody testa of a milkweed seed. However, some experimental media, such as homogenised peanut in agar, were as hard as the interior of a milkweed seed or a fresh peanut, and the behaviour of the stylets appeared to be substantially the same in hard media as it was in soft.

The cinephotomicrographic apparatus used is illustrated in Plate IA. The camera was driven by an electric motor, mounted on a heavy frame to prevent vibration and operated by a push-button switch. Records were taken on Kodak R 55 film, which is very fast and gave good contrast with lighting from a 75-watt pearl lamp and a shutter speed of 16 frames per second.

STYLET ACTION IN *ONCOPELTUS*

In artificial media, *Oncopeltus* stylets slid rapidly over one another, causing the tip of the stylet bundle to move continually back and forth over small distances. Individual cycles of forward and backward movement seldom returned the tip of the stylet bundle to the same position, and normally there was a progressive movement in one direction. The consistency of the substrate tended to affect the rate and magnitude but not the duration of individual stylet movements, so that cycles of forward and backward movements of the tip of the stylet bundle occurred about every quarter second, irrespective of the type of substrate. The sequences of individual stylet movements could be conveniently classified as "advancing", when the stylets were moving into a region not pierced before; "pumping", when the stylets were moving along tracks already made in the medium; and "retracting", when they were being withdrawn over some distance either prior to final withdrawal or to begin a new advance in some other direction. These three types of action alternated rapidly and continually. Normally the maxillae moved together; they were occasionally observed to slide over one another during both forward and backward movement, but this did not appear to be important in the mechanics of movement and it seldom occurred.

When the barbed tip of a mandible is located at the side of the maxillae (fig. 3A), the barbs stick outwards and backwards, increasing the girth of the bundle and, in solid media, anchoring it. On the other hand, if the tip of a mandible is to the front of the bundle (fig. 3B), the barbs curve over the tips of the maxillae giving the tip of the bundle its smallest girth and "streamlining" it for movement in either direction.

When the stylets were "advancing" into soft agar media, the maxillae were sometimes observed to lead, but in the hard media, attempts to lead with the maxillae were unsuccessful and the mandibles would come to the front and force their way ahead. One mandible advanced at a time, either alone or with the maxillae. When one mandible moved forward alone, it curved towards the opposite side of the stylet bundle; the resistance of solid media increased the sharpness of the curve and prevented deflection of the mandible when the other stylets followed and were guided to the one side (fig. 3E). On the other hand, when a mandible moved forward with the maxillae the latter overcame the tendency of the mandible to curve inwards, and progress was straight ahead (fig. 3D). The insect was thus able to control the lateral direction taken by the stylet bundle.

Weber's suggestion that the direction taken by the stylets is controlled by unequal thrusts on the maxillae would be possible only if the maxillae were tied at their tips, and if they led the stylet bundle during advance. However, it appears that in other Hemiptera, as well as in *Oncopeltus*, the maxillae can move separately (Zweigelt, 1915; Weber, 1930; Pesson, 1944), and that the mandibles lead during advance of the stylet bundle, at least in *Psylla* (Weber, 1928) and *Oncopeltus*. Whether the direction taken by the stylets is controlled in all Hemiptera in the manner described here for *Oncopeltus* would depend on whether the tendency of the mandibles to curve inwards is common to all; Weber's illustrations (1928) indicated that it is true of *Psylla* nymphs (fig. 1B).

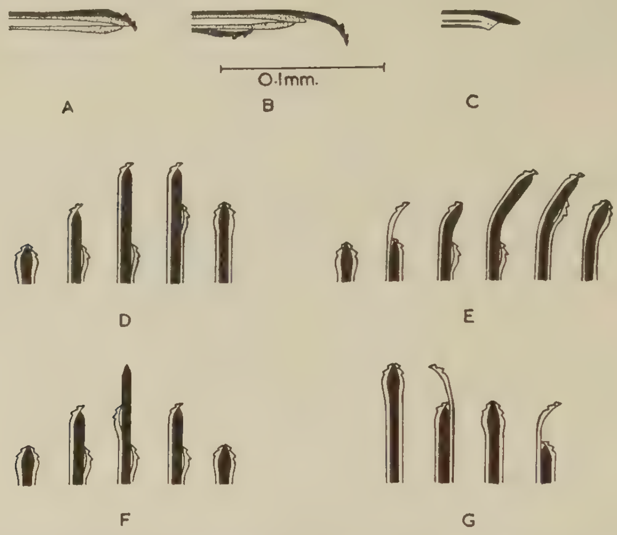

Fig. 3.—The stylet tips of *Oncopeltus* and idealised sequences of stylet movement. (A) and (B) Camera lucida drawings of dorsoventral views of the tip of the bundle. The mandibles are shown black, and the thickened walls of the maxillae, stippled. (C) Camera lucida drawing of a lateral view of the tip of a maxilla, showing the thickened point and the food and salivary canals above and below respectively. (D), (E), (F), (G) Diagrams of idealised sequences of movement (from left to right). The combined maxillae are shown black, and the mandibles in outline. For further explanation, see text.

"Pumping" involved forward and backward movements of the maxillae in the track of a previous advance, either alone or with one or other of the mandibles (fig. 3F). These movements were similar to the "advancing" movements sometimes observed in soft media, hence they are possibly best considered as the typical sequence of movement straight ahead when forward progress of the maxillae is not prevented by the resistance of the medium.

During typical "retraction", the tips of the maxillae were pulled back sufficiently to allow the mandibles to curve over the front of the stylet bundle, the maxillae continued to withdraw, bringing with them one mandible, and the other mandible was then withdrawn and the process repeated (fig. 3G). The other conceivable method of retraction, while maintaining the least possible girth, would be the retraction of the entire bundle with the tips of the mandibles curved over those of the maxillae. However, this would cause the greatest friction with the walls of the track, and it was never observed.

The typical retraction sequence was best seen during the rapid, final withdrawal from the substrate but, at other times, "pumping" movements would intervene and a gradual withdrawal occur without the tip of either mandible being left projecting alone beyond the stylet bundle. Sometimes, during a particularly rapid withdrawal, the tips of the maxillae would be pulled back far enough to become separated from the tips of both mandibles. This configuration of the stylets did not occur otherwise, *i.e.* never during forward movement, as proposed by Weber in the case of *Psylla* nymphs.

The sequences shown in figure 3 are idealised, and it was observed that any part of a sequence might be reversed or go straight into another. Plate Iʙ shows part of one of the series of cinephotomicrographs taken.

SUMMARY

The action of the stylets of the milkweed bug, *Oncopeltus fasciatus* Dall., can be investigated by cinephotomicrography while the insect feeds on films of agar gel containing sucrose. The stylets move rapidly back and forth while progressing through the substrate. Sequences of stylet movement can be characterised as " advancing ", " retracting " and " pumping ", the last referring to movement over a restricted distance in a previously made channel. During advance, one mandible leads, either alone or with the maxillae ; if projected alone, the mandible curves inwards, and the stylets following are thereby guided to the one side ; if the mandible leads with the maxillae, the latter overcome the tendency of the mandible to curve inwards, and progress is straight ahead. There is no evidence that, during advance, the tips of the mandibles ever come together appreciably in front of the tips of the maxillae, nor that the maxillae alone determine the direction taken by the stylet bundle, as suggested in a previous account of hemipterous stylet activity by Weber (1930).

ACKNOWLEDGMENTS

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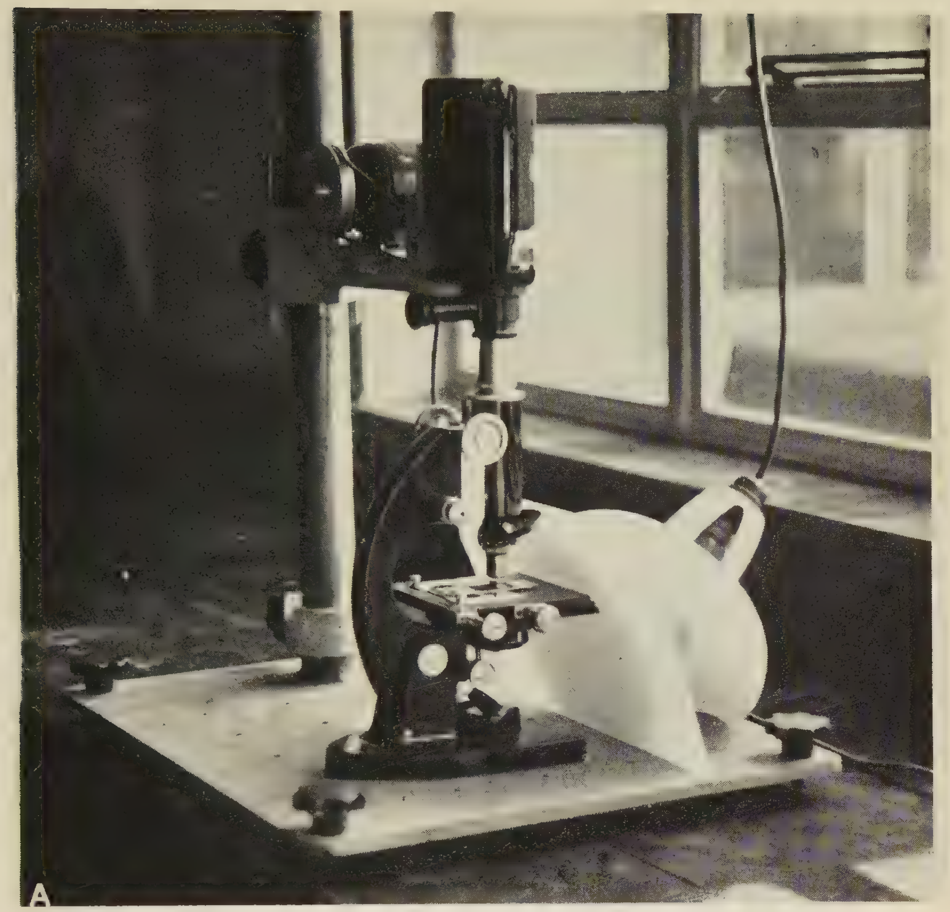
Book Notice

The Pursuit of Moths and Butterflies : an Anthology. By Patrick Matthews. 8vo. London (Chatto & Windus), 1957. Pp. 141, 36 pls. (4 col.). Price 30s.

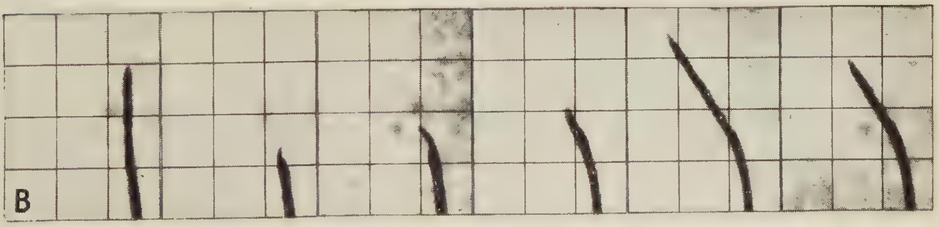
This work takes the form of an illustrated anthology of descriptive writings recording the pure pleasure of collecting and watching butterflies and moths, and of the fleeting exertions and excitements of the collector on an expedition.

The wide range of literature searched by the author has resulted in a work of unusual scope and fascination, including extracts from J. H. Fabre, W. H. Hudson, W. J. Holland, Colette, Virginia Woolf, A. Radcliffe Grote, William Beebe and many others. It takes the reader from Japan to Montenegro, and from Ruwenzori to the Arctic Circle, and it is fascinating to read how it is the greatest hardships in the most inaccessible places that are suffered with the greatest pleasure.

There are four coloured and thirty-two half-tone plates, the interest of which is enhanced by an appendix giving details of the background associated with some of them.



(A) The microscope and camera assembly used for cinephotomicrography of stylet action. The feeding pillory (fig. 2) is placed in position on the microscope stage.



(B) Cinephotomicrographs of *Oncopeltus* stylet movement in a sucrose-agar substrate. From left to right, successive positions of the stylets at 1/16th second intervals during a change of direction of movement: the maxillae retreat, the right mandible is thrust forward and the rest of the stylets then advance, guided in a new direction.

SYMBIOSIS AND *ANOBIUM PUNCTATUM* DE GEER

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Introduction

A summary of work carried out by Buchner, Karawaiew, Stein, Breitsprecher, Escherich, Heitz (Buchner, 1927) and later workers on symbiosis among plant-feeding insects shows that most insects feeding on plant tissues—particularly those utilizing cell walls of plants—must produce enzymes capable of digesting those walls, or have the assistance of micro-organisms of one sort or another to break down the cellulose and certain other plant constituents to a form that can be assimilated by insects. In Anobiids the micro-organisms have been identified as yeasts or Saccharomycetes, which have been recovered from special glands or caecal pouches on anterior and posterior ends of the mid-intestine, or adjacent to the reproductive organs in female beetles. During oviposition, special muscles contract to ensure that eggs are coated—at least posteriorly—with these yeast cells. Larvae, on emerging from eggs, normally eat part of the shells and consequently the yeast cells, which remain for some time free in the intestinal lumen but later invade the epithelial cells of the involuted portions of the intestines. Studies of sections indicated that during histolysis the yeast cells invaded the imaginal discs. Later, when the pupa began to show colour, the yeast cells filled the special pouches of the hind intestine of the future female beetles.

There is still a great deal of controversy as to the exact contribution made by symbionts to the welfare of the host insect, but opinion is conclusive that those insects harbouring symbionts develop more rapidly and completely when the micro-organisms are present than when absent. The present work does not determine the exact place of Saccharomycetes in *A. punctatum* nutrition, but it does confirm the findings of previous workers in indicating that yeast cells are essential for normal development of this insect.

Eggs of *A. punctatum* resemble in shape a perfect acorn and its cup. The " cup " is alveolate with minute pits, and slightly wider than the distal two-thirds, which is perfectly smooth and terminates in a short, blunt point. The alveolate end of the egg is the last to leave the ovipositor, and it appears that in doing so it becomes coated with yeast cells. Larvae of *A. punctatum*, on emerging from eggs, nearly always do so directly into timber and, as their heads are normally at the alveolate ends of eggs, they automatically eat the egg shell and yeast cells before entering the timber itself. This applies under natural conditions where eggs are wedged tightly into end grain of timber, or lie on their sides firmly wedged beneath rough splinters or surfaces of wood. Tests by the author showed that when eggs were on end with the alveolate end free of the wood surface, larvae turned and ate their way through smooth ends of eggs.

PROC. R. ENT. SOC. LOND. (A) 33. PTS. 1–3. (MARCH, 1958).

MATERIALS AND METHODS

This work was carried out from November, 1944 to April, 1946, and was divided into four separate tests. These were all carried out in small Prell (Peterson, 1937) cages containing kahikatea (*Podocarpus dacrydioides* A. Rich.) blocks measuring 2 in. × 1 in. × 1 in., all of which came from the same piece of timber. In Tests I and II, the blocks received no surface treatment and were left in a rough-sawn state. These two tests were designed to compare larval habits under more or less natural conditions with habits under the artificial conditions provided in the next two tests. In Test III, the blocks were dressed all round, and the end grain sealed with beeswax to prevent oviposition there ; the sides were bandaged with a single thickness of organdie muslin fixed in place with flour paste. The object of this test was to create an artificial surface that would compel beetles to deposit eggs in such a manner that the yeast cell ends of eggs were not touching wood. After many grades of fabrics had been tested, organdie muslin was found to be a suitable material which had the additional advantage that eggs were deposited singly instead of being laid in dense clusters or tightly-packed rows, as often occurred on blocks without special surface treatment. This particular muslin was selected because strands were free of loose " pile ", the mesh being slightly less than the width of *A. punctatum* eggs (0·35 mm.), and the strands were the same thickness as the length of eggs (0·55 mm.). Test IV blocks were treated in the same way as those in III, except that a thread of cotton was spirally wound round blocks before the muslin was pasted on. By raising the fabric on cotton threads in this way, it was found that eggs were always laid on their sides along cotton strands ; this peculiarity gave a direct comparison between eggs standing on end and those lying on their sides. In Test I, 14 cages each with one block were used ; in Test II, 15 cages each with one block, and in Tests III and IV, five cages each with three blocks. Three male and three female beetles were placed in each cage of Tests I and II, and eight of each sex in each of the cages of Tests III and IV. Cages were examined for numbers of eggs laid up to the 31st day after placing beetles in them.

Each day blocks were inspected under the microscope to ensure that too many eggs were not laid per block, to count the eggs that hatched and to note those showing different methods of larval emergence. Those showing sections eaten out of alveolate ends were removed, and intact eggs left in place for subsequent examinations. Final inspection took place 17 months after setting up experiments, and the results are expressed on the basis of the relationship between large or small larvae, and emergence through alveolate or non-alveolate parts of the egg respectively (see Table I.).

On the assumption that ingestion of yeast cells is necessary for normal larval development :

> (1) The difference between columns 1 and 2 (Table I), expressed as a percentage of those in column 1, gives the theoretical survival of normal larvae as shown in column 6, and column 4, expressed as a percentage of column 1, the actual percentage survival of normal larvae, and is shown in column 7.

TABLE I.—*Showing how the eating of alveolate ends of eggs influenced subsequent larval development in* Anobium punctatum *de Geer*

	1	2	3	4	5	6	7	8
			Larvae recovered alive			Large larvae only		
Test block surface	No. hatched eggs	No. eggs with alveolar ends intact	Small	Large	Total	Theoretical survival (%)	Actual survival (%)	Total survival (%)
I Rough sawn .	355	140	73	255	328	61	72	92·3
II Rough sawn .	487	161	57	356	413	67	73	84·8
III Sealed ends; muslin bandage only . .	1981	1843	281	142	423	7·0	7·2	21·3
IV Sealed ends; muslin bandage plus thread .	1848	0	0	1845	1845	100	99·8	99·8

(2) The figures in column 2 represent the total of underdeveloped or small larvae plus those that died. This latter figure should be given by the difference between columns 2 and 3.

(3) Figures in column 5, expressed as a percentage of those in column 1, give the total survival of both small and large larvae, and these are shown in column 8.

CONCLUSIONS

Table I shows that under more or less natural conditions (Tests I and II) one may expect that approximately 70 per cent. of the larvae hatching will develop normally in timber, as this is the proportion that ingests yeast cells on hatching. Comparison of figures in these two tests with those from Test IV shows a considerable difference, and it might be thought that the flour paste in the latter tests would partly account for this. However, this paste was used also in Test III, and if it did have an effect it was not significant in this case in increasing the number of normal larvae that developed. Further, there were no eggs from which larvae did not receive yeast cells in Test IV, whereas there were 39 per cent. and 33 per cent. of eggs in Tests I and II respectively, in which alveolate egg ends were intact after larvae tunnelled in. It is considered, therefore, that the difference is due to intake of yeast cells in the two different types of tests. The experimental error in counting eggs in Tests I and II was fairly great on account of roughness of timber surfaces, and this error could account for the discrepancy between theoretical and actual survival rates in these two tests as compared with the small difference in Test IV.

In Test III, 138 eggs had sections eaten out of alveolate ends, and this agrees reasonably closely with the 142 large larvae recovered.

A conspicuous feature of Tests I–III was that there were two distinct sizes of live larvae at the end of 17 months. The smaller larvae were less than one-third the size of the large ones. Since there were no small larvae in Test IV blocks, where all larvae had eaten part of the alveolate ends of eggs and, presumably, yeast cells, it is considered that the small live larvae in Tests I–III had managed to survive on a low nutritional plane without the assistance of yeast cells, but that large larvae had developed normally because they possessed yeast cells.

No larval dissections were carried out to verify the presence or otherwise of yeast cells; the above conclusions are based on whether or not larvae ate portions of alveolate ends of eggs where yeast cells were known to be present.

Summary

The experiments described here indicate that there is a close relationship between the presence of yeast cells on eggs and optimum development of larvae of *Anobium punctatum* de Geer, though larvae could survive on a low nutritional plane for 17 months in the absence of yeast cells.

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THE MODE OF REPRODUCTION OF *PTINUS CLAVIPES* PANZER FORM *MOBILIS* MOORE (= *P. LATRO* AUCT.) (COLEOPTERA : PTINIDAE)

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In a recent communication Moore, Woodroffe and Sanderson (1956) reported an unusual method of reproduction in the species then known as *Ptinus hirtellus* Sturm and *P. latro* Fab. They showed that *latro* was a parthenogenetic triploid, reproducing by gynogenesis after mating with *hirtellus* males, and suggested that the two should be regarded as forms of one polymorphic species. The cytological work on which these findings were based has since been described by Sanderson (*in press*). More recently Moore (1957) has shown that Fabricius' *latro* must be regarded as a synonym of *P. fur* Linnaeus and that *clavipes* Panzer is the first valid name for *hirtellus* Sturm ; the form *latro* auct. he has named *mobilis*. The present paper describes the general biological work which contributed to the published conclusions and includes also some more recent results. The names *clavipes* (for *hirtellus*) and f. *mobilis* (for *latro*) will be used throughout.

BREEDING EXPERIMENTS

The work originated as an attempt to obtain, for taxonomic purposes, authentic males of f. *mobilis* by breeding from the easily identifiable females (*see* Moore, *op. cit.* for plate) which, captured in the field, would presumably be fertilised. In this we received valuable assistance from the inspectors of the Infestation Control Division of the Ministry of Agriculture, Fisheries and Food, who sent in any live *clavipes* or f. *mobilis* which they discovered in the course of their duties, thus providing the material for the first culture. The few live female *mobilis* so obtained were provided with a food consisting of equal parts of wheatmeal and fishmeal, with 5 per cent. of dried yeast, and were kept in a 2-lb. jam-jar at 25° C. and 70 per cent. relative humidity. From this culture, set up in November, 1953, 17 larvae were obtained and these became adult in May, 1954 ; all were female. Six of them were kept without males until they died in November, 1954, and they produced no larvae. To the remainder 10 male *clavipes* were added and 21 larvae eventually appeared. These all became adult female *mobilis* by the end of December, 1954.

The culture conditions were then changed and the method described below was used in all subsequent work. Large jars (7 lb.) were charged with foodstuff to a depth of about three inches and a drinking " fountain " was embedded in the foodstuff. This consisted of a 3 inch × 1 inch tube of water with a rolled filter-paper inside, projecting about half an inch through a hole in the cork. A paper bridge was provided to enable the beetles to climb easily from the foodstuff to the top of the fountain. They drank from the projecting moist filter-paper and the water in the tube was replenished monthly. This arrangement seemed to provide exceptionally good conditions for breeding *mobilis*. A standard culture of this type, set up with 30–50 adults of each sex, the males being *clavipes*, produced about 2000 female *mobilis* of the next generation, whereas the use of smaller jars, even though the density of adults per unit area of food surface remained the same, resulted in a very weak culture or, occasionally, complete failure. At the same time, at the suggestion of Mr. R. W. Howe of this Laboratory, ovipositing adults were kept at 20° C. instead of 25° C., a temperature which he has found to be optimal for oviposition in several species of Ptinids. Under these conditions about 20,000 adults of f. *mobilis* have been reared but no male has so far been discovered. Also, no successful cultures were obtained without the addition of male *clavipes*.

MATING AND MATING BEHAVIOUR

Mating is very rarely observed in Ptinids. Mr. Howe, who has worked with many species at this Laboratory for about 12 years, has only very occasionally seen mounted pairs and the writer had never previously observed it. Against this background the mating response of *clavipes* males to *mobilis* females was remarkably vigorous. For several months after being set up, inspection of a standard culture at any time invariably revealed several pairs *in copulo*, whereas it was impossible to find a mating pair in insectary cultures of other species. Mating was observed in *clavipes* when males were first placed with virgin females which had been isolated for six weeks previously, but the reaction was much less marked than with *mobilis* females. This pronounced mating reaction was associated with definite postural behaviour on the part of the *mobilis* females. This comprised the bending of the fore legs and straightening of the hind legs until the insect was virtually " standing on its head ". This " calling " posture was often maintained for some considerable time, while the tip of the ovipositor was slowly extruded and withdrawn. This behaviour was of interest to other *mobilis* females, which sometimes appeared to imbibe fluid from the tip of the abdomen of those in the " calling " pose. The attitude was often almost universal in culture jars containing large numbers of virgin females. It was never observed in *clavipes* females.

OVIPOSITION AND EGG VIABILITY

Oviposition by mated *mobilis* females began about a week after mating was first observed. The eggs were laid loosely on or just beneath the surface of the foodstuff. In the act of oviposition the females adopted a posture which was the reverse of the " calling " posture—*i.e.* with fore legs straight and hindlegs bent, the body almost vertical and resting on the tip of the abdomen. While this attitude might be considered normal for an ovipositing Ptinid, it was not seen in other species. Possibly the oviposition of *mobilis* is slower than that of other species and the posture is thus more likely to be noticed.

One possible explanation of the production of one sex only in *mobilis* is that males die early in development. No obvious mortality occurred among the larvae, so it was considered advisable to check the viability of the eggs. This was done with both *mobilis* and *clavipes*, and approximately 80 per cent. of eggs hatched in each case. This contrasts with Howe's findings (Howe,

1955) for *clavipes* (= *hirtellus*) that " this species laid well but a large proportion of the eggs were infertile at every temperature used". The discrepancy may be due to the fact that Howe worked with isolated pairs, whereas this test was carried out under conditions in which repeated mating, which probably increases egg viability, was more likely to occur.

It has already been stated that cultures of virgin *mobilis* females invariably died out without producing larvae and usually few or no eggs were laid. However, it was discovered that virgin females would lay eggs if they were kept under exceptionally crowded conditions. Some 40,000 such eggs were collected and incubated and in the vast majority no development occurred. However, in two eggs development proceeded until the fully-formed first-stage larva was lying loosely inside the shell. One was dead when found but the other was alive when removed from the shell, though it died soon afterwards. About 20 other eggs developed until the brown larval mandibles were visible through the shell. Thus, in a very small proportion of eggs, development commences without the intervention of the male, but some factor prevents completion of the process. Under natural conditions the degree of crowding necessary to induce virgin females to lay probably never occurs.

The importance of the sperm in the reproductive process was investigated by sterilising *clavipes* males by exposure to gamma-radiation emitted by radioactive cobalt. This was carried out by the Technical Irradiation Unit at Harwell. Estimated dosages of five, ten and fifteen thousand röntgen were used. The insects survived the treatment well and length of life and mating behaviour were not affected. Irradiated males were mated with virgin females of both forms and in each case large numbers of non-viable eggs were produced. Towards the end of the experiment the appearance of a few larvae suggested that sterilisation of the males had not been permanent. However, the results indicate that live sperm play an essential part in the reproductive process.

RELATIONS WITH OTHER *PTINUS* SPECIES

Moore, Woodroffe and Sanderson (*op. cit.*) gave some evidence that a weak mating reaction occurred between males of *P. pusillus* Sturm and female *mobilis* and that a few larvae were produced. This was the result of one small-scale experiment, and was not considered conclusive. The point has since been tested by setting up a standard culture, using *pusillus* males, and it is now clear that the mating response is just as vigorous as between *clavipes* and *mobilis*, but production of larvae is very inferior, though the resulting adults are normal. The standard culture of *pusillus-mobilis* produced only about 100 larvae as opposed to about 2000 by an average *clavipes-mobilis* standard culture. A similar experiment using males of *P. fur* Linnaeus showed that the mating reaction was extremely weak. Only about a dozen instances of mating were noted during prolonged observation and most of these were made by one particular male during one half-hour period ; only two larvae were produced.

DISCUSSION

Reproduction in the Coleoptera is generally orthodox and very few examples of abnormal cytogenic mechanisms are known. One species, *Micromalthus* *debilis* Leconte, resembles the Hymenoptera and certain Homoptera in having haploid males. It also exhibits a peculiar cyclic type of parthenogenesis involving four kinds of reproductive females, three of them larval. Apart from this isolated example, abnormal reproduction has been reported only in the Otiorrhynchinae, in which many species, comprising a number of genera, show thelytokous, polyploid parthenogenesis. In some species both bisexual and parthenogenetic forms occur and in these cases the latter usually have the more northerly distribution (Suomalainen, 1950).

Reproduction in *Ptinus clavipes* f. *mobilis* is by thelytokous, triploid parthenogenesis and is, to this extent, similar to that of the Otiorrhynchine weevils but the details of the process—obligatory gynogenesis and striking mating behaviour involving males of two or three species—appear to have no precise parallel in the Coleoptera, nor, indeed, in the Insecta. Consequently the decision as to the formal status of the parthenogenetic triploid cannot be based on precedent and must inevitably be arbitrary. On the one hand, it can be argued that *clavipes* and *mobilis* are completely isolated genetically and are sufficiently different taxonomically to enable reliable identification to be made ; they should thus be regarded as distinct species. On the other hand, *mobilis* cannot reproduce without the intervention of the male, usually *clavipes*, and this situation cannot be fitted satisfactorily into any generally acceptable species concept. As Smith (1955) has pointed out, clones of any completely parthenogenetic organism are always genetically isolated. The status of a subspecies seems precluded by the absence of any geographic or ecological separation between the two—indeed, the necessity for mating rules out such separation. In the face of these conflicting arguments and in the absence of precedent, it was decided to regard *mobilis* (*P. latro* auct.) as a parthenogenetic form of *clavipes* (*P. hirtellus* Sturm).

The evolutionary significance of this highly abnormal method of reproduction is not clear. The parthenogenetic form cannot extend the geographic range of the species nor can it invade new habitats because of its complete dependence on the bisexual form. Moreover, there is no evidence that it can exploit existing habitats more effectively than the diploid. Indeed, its rarity suggests the opposite. The only explanation of its existence is that it represents a form which has arisen accidentally and persists in small numbers in a peculiar environment. It has been suggested that the Ptinidae are derived from the Anobiidae, from an ancestor of the present-day *Hedobia*, a very *Ptinus*-like Anobiid (Crowson, 1955). The Anobiidae are wood-borers, whereas no Ptinid is a true wood-borer ; thus, to quote Crowson (*op cit.* : 77) " it seems that the loss of the wood-boring habit was a fundamental factor conditioning the divergence of the Ptinidae as a family." The Ptinidae are dry-litter scavengers and, as such, are typical nest-dwellers, feeding on the accumulations of dried organic waste which, under natural conditions and in temperate climates, are found almost exclusively in the nests of birds, mammals and social insects. Many human activities, especially storage of food and clothing, have vastly increased the amount of food of a suitable nature which is now available to these dry-litter scavengers. Many of them, including most Ptinids, have consequently become pests of stored products and exist in warehouses and similar habitats as far larger populations than could normally occur in their natural habitats. One true Anobiid, *Stegobium paniceum* L., has developed similar habits (Woodroffe, 1952 ; 1953). It might reasonably be supposed that the stringent selection which would have eliminated the f. *mobilis* under natural conditions operates less decisively in such an artificial and peculiarly favourable environment, thus allowing the form to persist as a rare curiosity. It is, perhaps, significant that there are no reliable records of *mobilis* from entirely natural habitats.

SUMMARY

It has previously been shown that *Ptinus latro* auct. exists as females only and should be regarded as a gynogenetic, triploid form of *P. hirtellus* Sturm ; also, that *Ptinus clavipes* Panzer is the earliest valid name for *P. hirtellus* Sturm ; that *P. latro* Fabricius is a synonym of *P. fur* Linnaeus ; and that *P. latro* auct. must be known as *P. clavipes* f. *mobilis* Moore.

Breeding experiments designed to investigate the mode of reproduction of f. *mobilis* are described. The following main points were established :

(1) Females of *mobilis* will reproduce only after mating with males of *clavipes*, *pusillus* or *fur*. As regards production of larvae, the first named is very effective, the second only moderately so and the last almost ineffective. The progeny of these crosses were all *mobilis*.

(2) Egg viability, when *mobilis* females can experience repeated mating, is normal for a Ptinid. A very small proportion of eggs laid by unmated females show some development but do not yield feeding larvae.

(3) A remarkably vigorous mating response exists between *mobilis* females and males of *clavipes* and *pusillus* and is associated with a definite behaviour pattern on the part of the *mobilis* females.

(4) An experiment using sterilised males showed that viable sperm are essential for effective reproduction.

A comparison is made with other parthenogenetic Coleoptera and the uniqueness of the situation which exists in *mobilis* is emphasised. Reasons are given for regarding *mobilis* as a form of *clavipes*, and the evolutionary significance of the unusual method of reproduction is discussed.

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POPULATION NUMBERS IN A COLONY OF *LYSANDRA BELLARGUS* ROTT. (LEPIDOPTERA : LYCAENIDAE) DURING 1956

By G. A. N. Davis, J. F. D. Frazer and A. M. Tynan

During 1955 and 1956 an examination of some of the butterfly populations in a circumscribed area of the North Downs was carried out as part of the Kent Field Club survey of Burham Down (Frazer, McDermott, Morgan, Philp and Tynan, 1958). Before the second year's work had started, it was suggested that a colony of *Lysandra bellargus* Rott., a few miles from the area of the original work, should also be investigated, and that this might be particularly valuable in view of the recent alleged scarcity of this butterfly. This survey was undertaken during the month of June and the first three weeks of September, 1956.

Methods

The colony inhabited an area of rough grass downland (full National Grid reference TQ 51/751608) near the foot of Bluebell Hill, between Chatham and Maidstone. The site is on a slope facing south-east, roughly three acres in area, and isolated from all other suitable territory by roads, woods, cultivated fields, houses and gardens.

Visits were made to the colony as frequently as possible, and as many insects as possible captured, marked with cellulose paint (using a different colour for each visit) and then released again. This is the technique originally described by Dowdeswell, Fisher and Ford (1940), the number of marked insects recaptured on any one day being used to give an estimate of the population present on that day. The technique has been fully explained by Ford (1953). The results are here set out as shown by him, using an abridged form of table to omit days when no captures were made ; and the total numbers flying during the periods have been estimated by the method of Sheppard (*see* Ford, 1953).

Unfortunately, owing to a misunderstanding, no visits were made at the latter end of August, and *L. bellargus* was already flying when the first September visit was made. *Lysandra coridon* Poda was also found to be present in some numbers, although by then the colony a few miles along the Down showed very few insects (Frazer *et al.*, 1958). It was decided to examine the numbers of this species as well as of *L. bellargus*.

Results

The June emergence was found to be an explosive one. A visit in suitable weather on 28th May failed to disclose any of the species, while on the 31st they were flying in abundance. By 25th June it was only possible to find four males and seven females in about an hour.

The actual numbers of captures and recaptures are given in figures 1 (*L. bellargus*) and 2 (*L. coridon*). These are in the form of triangle diagrams, as originally used by Dowdeswell *et al.* (1940) and modified by Fisher and Ford

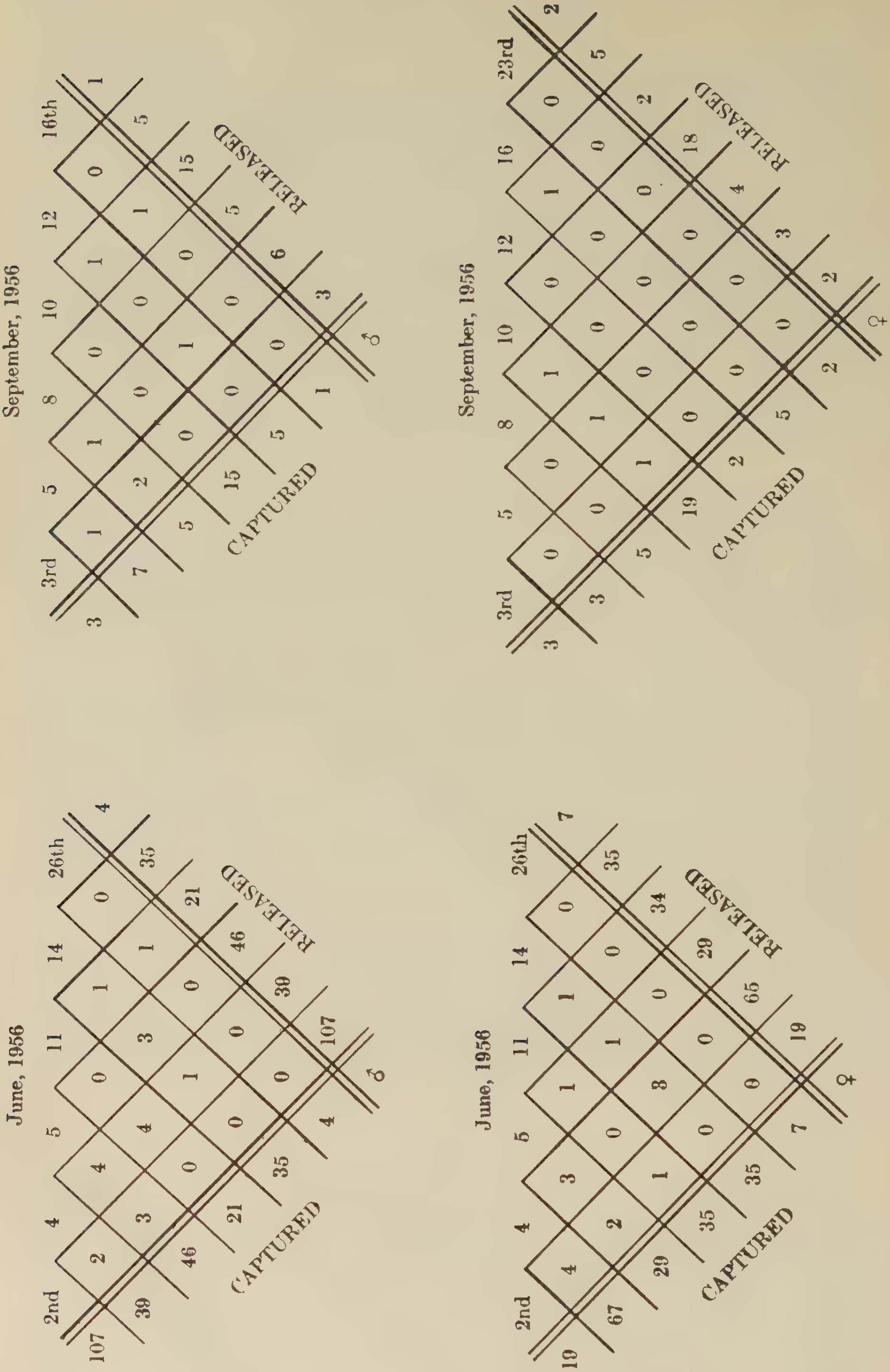

Fig. 1.—Triangle diagrams giving the recapture frequency of both sexes of *L. bellargus* in the two broods.

(1947). From each date run two diagonal columns, that slanting to the left giving the number of insects captured on that date, and that to the right the number then released. The figures outside the double lines give totals for each day. The figures inside the diamonds represent those insects marked and released on one day, and subsequently recaptured. For example, in figure 2 the number 5 in the results for males is at the intersection of columns from the

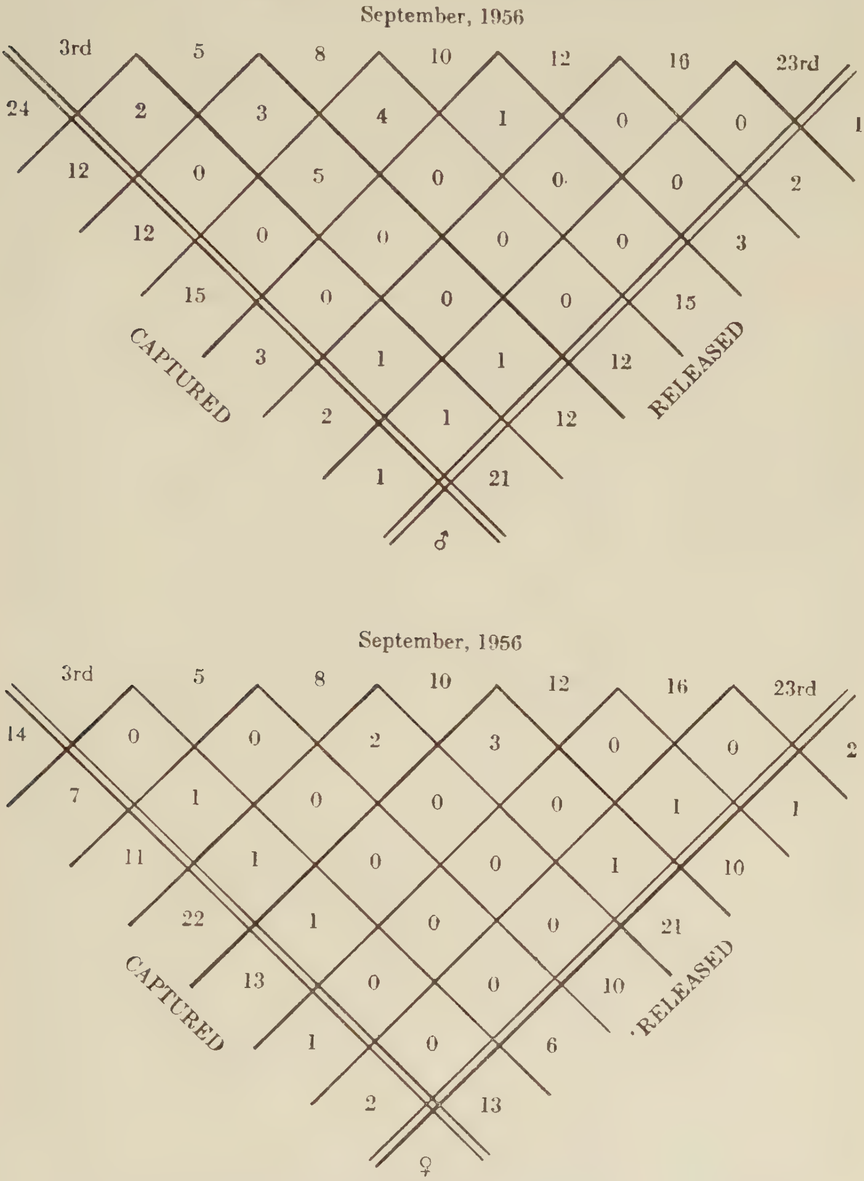

FIG. 2.—Triangle diagrams giving the recapture frequency of *L. coridon* (both sexes) during September.

TABLE I.—*Details of estimation of population numbers for* L. bellargus *in June and September,* 1956

Date	t	Released $\times r^t$	Σ_1	Σ_2	Total recaptures	Total days survived	Excess over expectation	Total captures	Estimated daily population	Date
A. Males r = 0·79 *in June,* 0·90 *in September.*										
June										June
25th	1	.	3·5466	53·9676	1	15	−0·22	4	18·0	26th
14th	12	2·0190	3·5466	14·9550	.	.	.	.	.	15th
13th	13	.	1·5276	11·4084	5	40	+2·65	35	229·3	14th
11th	15	0·6112	1·5276	8·3532	.	.	.	.	.	12th
10th	16	.	0·9164	6·8256	4	28	−1·80	21	209·2	11th
5th	21	0·3254	0·9164	2·2536	.	.	.	.	.	6th
4th	22	0·2179	0·5910	1·3372	7	13	−2·84	46	695·2	5th
3rd	23	.	0·3731	0·7462	2	4	0	39	248·2	4th
2nd	24	0·3731	0·3731	0·3731	.	.	.	.	.	3rd
Sept.										Sept.
15th	1	.	16·0529	107·8797	0	0	0	1	.	16th
12th	4	3·279	16·0529	66·4420	.	.	.	.	.	13th
11th	5	.	12·7739	43·6681	1	2	−1·42	5	181·6	12th
10th	6	7·968	12·7739	30·8942	.	.	.	.	.	11th
9th	7	.	4·8059	18·1243	0	0	0	15	>154·3	10th
8th	8	2·151	4·8059	13·3184	.	.	.	.	.	9th
7th	9	.	2·6549	8·5125	3	11	+1·38	5	10·9	8th
5th	11	1·881	2·6549	4·2027	.	.	.	.	.	6th
4th	12	.	0·7739	1·5478	1	2	0	7	19·2	5th
3rd	13	0·7739	0·7739	0·7739	.	.	.	.	.	4th
B. Females. r = 0·92 *in June,* 0·91 *in September.*										
June										June
25th	1	.	40·605	696·545	0	0	0	7	.	26th
14th	12	12·87	40·605	249·890	.	.	.	.	.	15th
13th	13	.	27·735	209·285	5	42	−4	35	573·8	14th
11th	15	9·738	27·735	153·815	.	.	.	.	.	12th
10th	16	.	17·997	126·080	2	15	+1	35	1195	11th
5th	21	5·037	17·997	36·097	.	.	.	.	.	6th
4th	22	10·39	12·96	18·10	5	9	+2	29	470·3	5th
3rd	23	.	2·57	5·14	4	8	0	67	368·5	4th
2nd	24	2·57	2·57	2·57	.	.	.	.	.	3rd
Sept.										Sept.
22nd	1	.	10·3817	124·8926	0	0	0	2	.	23rd
16th	7	2·576	10·3817	62·6024	.	.	.	.	.	17th
15th	8	.	7·8057	52·2207	1	4	−2·7	5	83·1	16th
12th	11	0·7079	7·8057	28·8036	.	.	.	.	.	13th
11th	12	.	7·0978	20·9979	0	0	0	2	.	12th
10th	13	5·276	7·0978	13·9001	.	.	.	.	.	11th
9th	14	.	1·8218	6·8023	3	14	+2·8	19	43·3	10th
8th	15	0·9707	1·8218	4·9805	.	.	.	.	.	9th
7th	16	.	0·8511	3·1587	0	0	0	5	.	8th
5th	18	0·5484	0·8511	1·4565	.	.	.	.	.	6th
4th	19	.	0·3027	0·6054	0	0	0	3	.	5th
3rd	20	0·3027	0·3027	0·3027	.	.	.	.	.	4th

t is days' interval from date of release till latest day of capture.

r is survival rate.

Σ_1 and Σ_2 are the progressive sums of the entries in the preceding columns from the bottom.

[For full explanation *see* Fisher and Ford, 1947].—[ED.].

5th and 10th September. Thus, five insects out of a total of 12 released on the 5th were recaptured in a total haul of 15 on the 10th.

Table I gives the results on population numbers of *L. bellargus*, and Table II those on *L. coridon*, as estimated from figures 1 and 2. It is noteworthy that the mean daily death rate was around 10 per cent. in *L. bellargus*, but was double this for males in June. The use of Sheppard's method on these figures gives a total first brood population of some 2700 males and 700 females. Sheppard's technique involves the adding together of the daily population numbers and multiplying this total by the proportion of the population dying each day. Thus, any unusually high figures on a single occasion are smoothed out, and a truer picture given of the whole population over the period. This accounts for the fact that the total female population given here is less than that estimated for one day in Table I. The data are inadequate for any accurate estimation of the September populations, but it seems as if the second brood of *L. bellargus* comprised only one-fortieth the numbers of the first. *L. coridon* (then at the end of its flight period) was about twice as plentiful as *L. bellargus*.

TABLE II.—*Details of population estimates for* L. coridon *in September*, 1956

Date	t	Released $\times r^t$	Σ_1	Σ_2	Total recaptures	Total days survived	Excess over expectation	Total captures	Estimated daily population	Date
A. Males.	$r = 0{\cdot}86$.									
Sept.										Sept.
22nd	1	.	6·4505	92·2072	2	38	+9·4	1	3·8	23rd
16th	7	0·6958	6·4505	53·5042	.	.	.	.	.	17th
15th	8	.	5·7547	47·0537	1	13	+4·8	2	38·5	16th
12th	11	0·571	5·7547	29·7896	.	.	.	.	.	13th
11th	12	.	5·1837	24·0349	1	2	−2·6	3	95·0	12th
10th	13	2·112	5·1837	18·8512	.	.	.	.	.	11th
9th	14	.	3·0717	13·6675	9	33	−7·0	15	42·3	10th
8th	15	1·249	3·0717	10·5958	.	.	.	.	.	9th
7th	16	.	1·8227	7·5241	3	9	−3·4	12	81·4	8th
5th	18	0·7947	1·8227	3·8787	.	.	.	.	.	6th
4th	19	.	1·0280	2·0560	2	4	0	12	105·9	5th
3rd	20	1·028	1·0280	1·0280	.	.	.	.	.	4th
B. Females.	$r = 0{\cdot}81$.									
Sept.										Sept.
22nd	1	.	3·3227	42·7223	2	24	−1·7	2	4·1	23rd
16th	7	0·2289	3·3227	22·7861	.	.	.	.	.	17th
15th	8	.	3·0938	19·4634	0	0	0	1	.	16th
12th	11	0·9851	3·0938	10·1820	.	.	.	.	.	13th
11th	12	.	2·1087	7·0882	4	15	+1·6	13	85·9	12th
10th	13	1·357	2·1087	4·9795	.	.	.	.	.	11th
9th	14	.	0·7517	2·8708	3	11	−0·5	22	105·3	10th
8th	15	0·4241	0·7517	2·1191	.	.	.	.	.	9th
7th	16	.	0·3276	1·3674	1	5	+0·8	11	156·3	8th
5th	18	0·1353	0·3276	0·7122	.	.	.	.	.	6th
4th	19	.	0·1923	0·3846	0	0	0	7	.	5th
3rd	20	0·1923	0·1923	0·1923	.	.	.	.	.	4th

DISCUSSION

Apart from the explosive nature of the June emergence, the figures for the first brood population are of interest as showing roughly four times as many males as females. In the allied *L. coridon*, figures for both 1955 and 1956 in a colony a few miles away (Frazer *et al.*, 1958) show a similar preponderance of males, although in the latter case it is only of the order of two to one. So far as is known, no other figures have been obtained for population numbers in the genus *Lysandra*, and it would be interesting to know if this male preponderance occurs also in other species. Such an abnormal sex ratio could be the result either of abnormal distribution of gametes at fertilisation, or of selective elimination of one sex during the early stages.

The relatively small numbers of the second brood of *L. bellargus* may probably be associated with the rather dull and wet summer, the majority of larvae having preferred hibernation to pupation in August.

The *L. coridon* population is of interest, showing relatively high numbers of insects still in fresh condition at a time when only a few very worn specimens were flying in the colony a mere mile or two away (Frazer *et al.*, 1958). This may perhaps point to a later emergence being associated with a less sheltered environment, but the matter requires further investigation in the years to come. The aspect of the site could be relevant to the production of only a small second brood of *L. bellargus*.

SUMMARY

1. A small isolated colony of *L. bellargus* Rott. has been investigated and the first brood numbers estimated as 2700 males and 700 females. Only about one-fortieth of these numbers were flying in September.

2. *L. coridon* was also present in the area in September, being remarkably late when compared with another colony a mile or two away. The population density was about double that of *L. bellargus*.

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COLEOPTERA OF MEDICAL INTEREST IN THE SUDAN REPUBLIC

By D. J. Lewis[1]

(*Care of the British Museum* (*Natural History*))

Beetles of many species are encountered by doctors and public health workers in the tropics and sent to entomologists with requests for identification and information about their significance. Species in the Sudan which have elicited such enquiries, or may do so, are recorded below under their families, and the ways in which they affect man—including the assistance given by scavengers which remove dung—are discussed in a later section.

Carabidae

Clivina grandis Dejean was common in cow dung at Wad Medani, and *Parasiopelus lucens* Putz and a species of *Pheropsophorus* were found in the same situation in July and November respectively.

Dytiscidae

Eretes sticticus (L.), which is widely distributed in warm regions (Balfour-Browne, 1951), occurs at El Obeid (Ebner, 1923) and many other places in the Sudan. Specimens were received from Port Sudan, where they had been found in a swimming bath and possibly mistaken for species of aquatic Hemiptera which sometimes bite people (Herms, 1950).

Staphylinidae

Paederus is a large cosmopolitan genus (Bequaert, 1921), most species of which contain a vesicating fluid that has been regarded as a substance different from the cantharidin of Meloidae (Patton and Evans, 1929). Gordon (1925), Pavlovsky and Stein (1927), and Roberts and Tonking (1935) studied, in Africa, the blistering action of *P. sabeus* Erichson, *P. fuscipes* Curtis and *P. crebripunctatus* Eppesheim respectively, and Théodoridès (1950*a*, *c*; 1951) reviewed other work in Africa and the rest of the world. *P. sabaeus* is common on swamp grass at Kosti and Sennar, and has been found at Danagla, Loa and Mvolo. When a specimen was rubbed on the skin experimentally it produced a large area of small painful blisters, but in the Sudan, and probably in many parts of Africa, *Paederus* beetles are not generally recognised as potentially harmful. Ebner (1928) recorded *P. fauveli* Quedenfeldt, *P. fuscipes* and *P. plagiator* Kolbe from the Sudan; Bernhauer (1927, 1937) described *P. darfurensis*, *P. steeleanus* (found recently at Guldo and Kelling) and *P. sudanensis* from Sudan specimens; and *P. parcepunctatus* Bernhauer and *P. scabripennis* var. *usticollis* Fauvel have been found at the Khor Yabus and Yambio respectively.

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Several brown and green, or brown and black, Staphylinids, such as *Zyras speciosus* Er., *Diatrechus* sp. and *Philolonthus paederomimus* Epp., can be mistaken for *Paederus* in the field.

HISTERIDAE

Hister memnonius Er. and *H. gehini* Marseul were common in cow dung at Wad Medani, and *H. bimaculatus* L. has been found there in July.

DERMESTIDAE

Anthrenus vorax Waterhouse, a nearly cosmopolitan species, is common in the Sudan, and its larvae, popularly known as woolly bears, can do much damage to woollen clothes (King, 1908, 1918). Hinton (1945) attributes the tendency of this and related species to feed on such materials to their tolerance of dryness, and points out that species and individuals of this genus are numerous in the Sahara and other arid regions. *Dermestes maculatus* Degeer (synonym, *D. vulpinus* Fabricius), a cosmopolitan species (Hinton, 1945), was recorded from the Sudan by Gredler (1877), King (1908) and Ebner (1928), and has often been found damaging skins. *Trogoderma granarium* Everts, a widely distributed pest of grain and cereal products, has been found at Khartoum.

CLERIDAE

Necrobia rufipes (Degeer), which preys on Dermestids (Hinton, 1945), is another nearly cosmopolitan beetle sometimes found in food in the Sudan. Infestation of the human urinary tract by a larva, possibly of this family, was reported by Archibald and King (1919), and cases have been recorded from other countries by Théodoridès (1950*b*).

BOSTRYCHIDAE

Rhizopertha dominica Fabricius, a cosmopolitan pest of grain (Busvine, 1951; Darling, 1951), is widely distributed in the Sudan and common in the north.

ELATERIDAE

A larva, possibly of a species of *Alaus*, was received in 1949 from Mafaza, where it had been found in a recently passed human stool.

TENEBRIONIDAE

Alphitobius diaperinus Panzer, a widely distributed species which occurs in flour (Busvine, 1951), has been found in a bedroom at Wad Medani, and had probably bred in a large mass of bat-droppings which had accumulated in the roof. Larvae and adults of this species were found in a pigeon cote in the same town, and the beetles were said to have attacked the young birds. A species of *Gonocephalum* sometimes enters houses in large numbers during the rains. *Latheticus oryzae* Waterhouse, *Tribolium castaneum* Herbst and *T. confusum* Duval are widely distributed species which occur in flour and are found at Khartoum. *T. castaneum* has been found damaging flies received for identification, and *T. confusum* is liable to attack museum specimens (King, 1908). A species of *Tenebrio* has been found in cow manure at Wad Medani and *Zophosis quadrilineata* Olivier in the paunch contents of a camel at El Hilla.

MELOIDAE

De Marseul (1872), Gredler (1877), Balfour (1904), Borchmann (1917) and Chalmers and King (1917) recorded several species from the Sudan, and many are now known to occur, particularly in the centre of the country where some of them are abundant in the rainy season. It is not known why Meloids are so numerous; the larvae of many species parasitise grasshoppers, which are numerous in the Sudan, and it may be that suitable hosts are plentiful and that, under the prevailing semi-desert conditions, many of the triangulin larvae escape attack by predators and are able to find their hosts.

Some of the species damage vegetables or trees, and some are troublesome blister beetles. According to Wigglesworth (1953) the blistering substance, cantharidin, may vary from 3 to 10 per cent. in different species and is discharged from several parts of the body. Chalmers and King (1917) reported that two species of blister beetles usually appeared in August at Khartoum and were much more numerous in some years than others. They also remarked that the beetles rested in cracks in the soil during the heat of the day, and that on one occasion an individual of one species failed to cause a blister. *Epicauta aethiops* Latr., a pest of vegetables (Tothill and others, 1948), and *Cyaneolytta sapphirina* Mäklin are among the commonest species in the country and are sometimes abundant in the rains at Wad Medani, where many of them enter houses in the evenings by crawling beneath doors. Adults of *C. sapphirina* are attracted to the bodies of those which have been crushed. The writer has tested the blistering powers of several species, and found that some exude blistering fluid only when very firmly pressed, and that some, even when crushed, cause little harm. Among the species able to cause blisters are the two mentioned above and *C. tenuicollis* Pall., *Cylindrothorax spurcaticollis* Fairmaire, *Mylabris tigrina* Klug, *Psalydolytta jaloffa* Castelnau and a species of *Sybaris*. *P. aegyptiaca* Mäkl. and *M. dilloni* Guérin appear to cause little or no blistering. The blisters induced by the common Meloids are painless but may last several days; they burst easily, so, as Matheson (1950) points out, they should be pricked and covered with an antiseptic dressing.

Göldi (1913) and Théodoridès (1950*c*, 1956) have referred to the danger of drinking liquids containing Meloid cantharidin, and several cases of suspected poisoning by Meloids have been reported in the Sudan (*Sudan Medical Service Annual Reports*). Specimens of a species of *Mylabris*, possibly *bifasciata* Deg., were once received from the south where powdered beetles of the same species were believed to have been placed in beer which was drunk by a man who died 12 hours later.

SCARABAEIDAE

A specimen of *Catharsis sesostris* Dej. was received from the Nuba Hills with the report that it had been passed in a human stool.

RUTELIDAE

Adorus emarginatus Ohaus was found in cow dung at Wad Medani.

APHODIIDAE

Aphodius discolor Er. occurs in cow dung at Wad Medani.

COPRIDAE

The green and copper species *Gynmopleurus bicolor* Latr. has been observed by day in the rainy season at Wad Medani. It was rapidly removing fresh human excreta, rolling the material into a ball in the manner of many members of this family. *Onthophagus catta* F., a widely distributed species (Paulian, 1948), occurs in cow dung in the same area, and a species of *Cheironitis* was found in the paunch contents of a camel at El Hilla.

SOME WAYS IN WHICH BEETLES AFFECT MAN

Théodoridès (1951) has discussed many ways in which beetles can affect man, and some are exemplified in the following notes which refer, by the names of families, to the species mentioned above.

Blister beetles, of the families Staphylinidae and Meloidae, have been discussed above, and reports mentioned of internal poisoning by some species.

The three known cases of canthariasis in the Sudan were caused by an adult of a species of Scarabaeidae (possibly a case of rectal infestation like those of small Scarabaeids in India reported by Patton, 1931) and two larvae which may have belonged to the Cleridae and Elateridae.

A beetle said to attack young pigeons belongs to the Tenebrionidae, which include a species reported by Théodoridès (1951) to kill young birds.

Among cosmopolitan species which eat human food are members of the Bostrychidae, and of the Dermestidae and Tenebrionidae, which include species that attack clothing and insect specimens.

Several species of beetles destroy harmful insects (West, 1951), and members of the Histeridae and Carabidae are believed to kill some house-fly larvae in the Sudan.

Miller (1954) has pointed out that scavenging beetles can remove large quantities of mammalian excreta in which house flies could breed. Although it is not always easy to demonstrate competition for food among insects in dung (Laurence, 1954), there is no doubt that some beetles in the Sudan play an important part in the control of house-fly larvae by eating dung and scattering some so that it dries in the sun. In the early part of the rainy season at Wad Medani, for instance, house flies are surprisingly scarce (Lewis, 1957) and one can see many beetles rapidly removing the breeding material. In August beetles appeared to remove human faeces and cow dung almost completely in 24 hours and three days respectively. Many house-fly larvae were found in dung from which beetles had been excluded. Scavengers, which were found during a few observations, belong to the families Tenebrionidae, Rutelidae, Aphodiidae and Copridae, and include genera mentioned among scavengers by Miller (1954), and a species of *Aphodius*, a genus to which the commonest Egyptian dung-eating beetle belongs (Hafez, 1939).

Various other ways in which beetles attract attention are by biting (a few unidentified species), entering swimming baths (Dytiscidae) and houses (Tenebrionidae), and occasionally by eating a few young *Gambusia* fish used for mosquito control (larvae of Dytiscidae).

SUMMARY

This paper contains records of beetles in the Sudan which cause blisters and canthariasis, eat human food and various materials, destroy dung in which house flies breed, probably eat fly larvae, and affect man in various other ways.

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HEMIPTERA OF MEDICAL INTEREST IN THE SUDAN REPUBLIC

By D. J. Lewis[1]

(*Care of the British Museum (Natural History)*)

The distribution of the two species of bed-bug in the Sudan was described by Lewis (1949); the present paper adds to this and records a number of minor pests, most of them plant sucking or predaceous species which sometimes cause annoyance by biting—piercing or partly piercing—human skin, and a few other examples of the relation between Hemiptera and man.

Initials in brackets refer to collectors mentioned in the section on acknowledgments.

Cydnidae

Geotomus pygmaeus Dallas, which is found at Wad Medani, is one of the Hemiptera which sometimes enter houses and earn the name of stink bugs.

Pentatomidae

Agonoscelis versicolor Fabricius, known in Arabic as the *andat*, is a pest of millet, and is sometimes collected and boiled for fat or distilled for tar (Tothill and others, 1948 : 314). The tar, known as *gutran el andat*, is said to be useful for treating camel mange, and Mr. L. George has given me an account of the method of preparing it, which he observed in Kassala Province in 1942. The bugs had gathered in trees, and all the people of Babanusa and El Buweida villages were busy in the early morning brushing the bugs on to mats and taking them to the villages in sacks. They were killed with boiling water and crushed on a millet-grinding stone or between two flat stones, boiled with a little water, and placed in a twisted cloth or *malwaya* from which an oily liquid was squeezed out. This was put in a jar, and when oil rose to the top it was skimmed off and boiled to remove traces of water, the final product being brown and smelling strongly like the *andat*. People near Wad Bakr were busy harvesting, and therefore used another method which yielded an inferior gutran. The bugs were placed over a fire, in an inverted narrow-necked clay vessel out of which liquid dripped and was collected.

Aethemenes chloris Westwood is another of the Pentatomids which assemble in large numbers. It occurs in the central rainlands and gathers in clusters in the isolated rocky hills such as Ghadambaliya, where it causes much annoyance by entering houses (R. V. J.). This species also occurs at Lui in the southern Sudan, where it is eaten by human beings, as are a clustering species in Southern Rhodesia (Bodenheimer, 1951) and some species in Assam (Strickland, 1932). *Piezodorus teretipes* Stål has been found in a house at Wad Medani.

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A species of *Mecidea* bit a man at El Hobagi in the north-western desert region (H. J. M.)

LYGAEIDAE

The small pale waxy-looking bug, *Leptodemus bicolor* Lindberg var. *ventralis* Lindberg is sometimes troublesome in the desert area around Wadi Halfa, and occurs in Egypt (Priesner, 1953). On 8th October, 1944, it was biting people at six railway stations south of Wadi Halfa and was said to cause irritation and fever (S. M. M.). On 19th August, 1948, specimens were taken while biting people on the aerodrome and near cultivated land near Wadi Halfa, and sent for identification by the Public Health Inspector (M. O. Z.). Bugs which are probably of this species have been received from Uweinat, where they were thought to be sandflies, and from Kufra Oasis in the Libyan desert. The bite of another Lygaeid, *Leptodemus bicolor* Iak, in Cyrenaica is said to be worse than that of a sandfly (Bergevin, 1925). *L. minutus* (Jackowleff) is reported by Foley (1929) to attack people in the Hoggar.

A species of *Nysius* and one of *Orthaea* (*Pamera*) have been seen to prick human skin at Wad Medani, the latter causing some irritation.

PYRRHOCORIDAE

A nymph of a species of Pyrrhocorid was found in the burrow of a ground squirrel at Wad Medani (H. H.), but it is not known if the bug had any association with this animal.

REDUVIIDAE

Among species which have been known to inflict a painful bite when accidentally disturbed are *Eremovescia lewisi* Miller (1951) at Wad Medani and another Reduviid at Mvolo.

Pasira basiptera Stål was found to pierce human skin at Wad Medani.

Two species of *Triatoma* were taken in tropical Africa by Emin Pasha, who spent many years in the Sudan, and described by Neiva (1911), but their place of origin is not known.

CIMICIDAE

Additional localities for the tropical bed-bug, *Cimex hemipterus* (Fabr.), are Kajo Kaji, Mvolo and the Saburi Hills, and, for *C. lectularius* L., Kelling, Kronga, Suni, Torme (all on Jebel Marra), Durraba and Damira el Tom.

Leptocimex vespertilionis Ferris and Usinger, 1957, is very similar to the spider-like *L. boueti* Brumpt, 1910, a parasite of man in North-west Africa, which has been erroneously referred to by Herms (1950) as " *C. boueti* Joyeux, the tropical bed-bug of Africa and South America ". *L. vespertilionis* is only known from the Sudan Republic, where it has been found at Zeidab (the type locality) and Khartoum. Bugs which are almost certainly of this species have been taken at Roseires, and in a bat roost behind some shutters on the Research Farm library at Wad Medani. On one occasion complaints of bugs in a club at Wad Medani led to the discovery of *Leptocimex* in a bedroom and bats in the roof.

Loxaspis miranda (Rothschild) has been found in a bat-infested store at Gogrial (P. Z. M.).

Kassianoff (1956) suggested that, from among the many Cimicid parasites of animals, three species, *C. hemipterus*, *C. lectularius* and *L. boueti* have parasitised man and flourished in the favourable environment of human dwellings. Although insects have been studied in the Sudan for 60 years, only one report has been received of *Leptocimex* entering a room, and it is likely that *L. vespertilionis* only makes occasional brief incursions into houses. Lewis (1949) found that *C. lectularius*, although a long-established parasite of man, was still spreading in the Sudan as a result of the development of communications. *C. hemipterus* occurred mainly in remote districts such as the Nuba Hills, and it is surprising that it was not seen during recent collections on the massif of Jebel Marra.

Crassicimex sexualis Ferris and Usinger is only known from Ikotos, where Mr. J. Owen found it on a bat.

ANTHOCORIDAE

King (1906) gave a preliminary description of a " Reduviid " which inflicted a painful bite on October evenings, and published a figure of it, which has been reproduced by Brumpt (1910) and Villiers (1952). Brumpt (1910) named it *Anthocoris kingi* without further description. *Piezostethus afer* Reuter has been known to bite, causing irritation and swelling, at Wad Medani.

POLYCTENIDAE

Eoctenes intermedius (Speiser) (=*eknomicus* (Kellog and Paine)) was found on a bat at Khartoum, according to Kellog and Paine (1911).

MIRIDAE

Camptotylus yersini Mulsant and Rey was found biting out of doors at Damer, and a species of *Psallus* was seen trying to pierce human skin at Wad Medani. *Creotiades pallidus* Rambur, a pest of cotton, sometimes bites people in the field at Tokar (A. G.).

BELOSTOMATIDAE

Lethocerus niloticus Stål is sometimes received for identification because its large size and conspicuous appearance attract attention. It kills a few of the *Gambusia* fish which are kept in stock ponds at Wad Medani for mosquito control.

JASSIDAE

When cotton was sprayed at night in the Gezira to kill Jassids the insects sometimes inflicted irritating bites on the operators of the machines. A species of *Erythroneura* and one of *Deltocephalus* were seen at Wad Medani, piercing and probing the skin respectively. *Euscelis curtipes* and a bug which may be an *Aconura*, according to Myers (1929), were described by Lindberg (1927) from specimens said to have sucked human blood in October at Khartoum. *E. vulnerans* Bergevin has been found biting there, and another species probed human skin at Wad Medani. *Thamnotettix cellulosa* was described by Lindberg, who reported that it sucked human blood at Khartoum, and two species of this genus were said to bite at Wad Medani.

THE OCCASIONAL BITING OF MAN BY HEMIPTERA

Species which occasionally pierce the human skin have been discussed by Blacklock (1923), Myers (1929), Usinger (1934) and Herms (1950), and it appears that the habit is partly due to hunger and to the attraction of human sweat. These causes probably operate in the Sudan, where most of the above-mentioned examples were obtained out of doors in the desert or semi-desert regions of the country, or indoors at Wad Medani, where they had probably become hungry while flying round lights. The biting species are distributed among six families and, as Myers (1929) found, are particularly numerous among the Jassidae. It is likely that many other species sometimes bite but have not been collected. Many of the bugs do not succeed in sucking blood, but some of them are much more irritating than certain blood-sucking flies.

SUMMARY

Most of the species recorded are minor pests and include Pentatomids, which enter houses, and members of the Pentatomidae, Lygaeidae, Reduviidae, Anthocoridae, Miridae and Jassidae which sometimes cause irritation by piercing, or trying to pierce, the human skin.

Four species of Cimicidae occur in the Sudan.

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BOOK NOTICES

Annual Review of Entomology. Edited by E. A. STEINHAUS. Vol. 2. 8vo. Palo Alto, California (Annual Reviews Inc.), 1957. Pp. viii + 407. Price $7.00.

The second volume of this *Review* contains twenty papers dealing with the following subjects :

Digestion in insects, *D. F. Waterhouse*.

Some aspects of intermediary metabolism of carbohydrates in insects, *M. Rockstein*.

The physiology of insect cuticle, *V. B. Wigglesworth*.

The comparative morphology of the insect head, *E. M. DuPorte*.

Cytogenetics and systematic entomology, *M. J. D. White*.

The taxonomic significance of the characters of immature insects, *F. I. van Emden*.

Caste determination in social insects, *M. V. Brian*.

Dynamics of insect populations, *M. E. Solomon*.

The synoptic approach to studies of insects and climate, *W. G. Wellington*.

Insect migration, *C. B. Williams*.

Recent advances in veterinary entomology, *A. W. Lindquist* and *E. F. Kipling*.

Transmission of disease agents by phlebotomine sand flies, *S. Adler* and *O. Theodor*.

Genetics of insect resistance to chemicals, *J. F. Crow*.

The mode of action of insecticides exclusive of organic phosphorus compounds, *P. A. Dahm*.

Chemistry and mode of action of organophosphorus insecticides, *E. V. Spencer* and *R. D. O'Brien*.

The behaviour of systemic insecticides applied to plants, *S. H. Bennett*.

Aerial application of insecticides, *F. E. Weick* and *G. A. Roth*.

Cotton insects and their control in the United States, *J. C. Gaines*.

Insecticidal control of the spread of plant viruses, *L. Broadbent*.

Pollination of alfalfa and red clover, *G. E. Bohart*.

Each article is followed by a list of references to the literature cited and an author and subject index is included at the end of the volume.

A Textbook of Entomology. By HERBERT H. ROSS. 2nd ed. 8vo. New York (John Wiley) ; London (Chapman & Hall), 1956. Pp. xi + 519, 402 text-figs. Price 62*s*.

This is the second edition of a work which first appeared in 1948, and is intended to provide a balanced introduction to modern entomology.

The new edition incorporates the advances made in the knowledge of insect physiology, ecology and evolution in the last ten years. Additional keys and many new drawings are included.

As in the earlier edition, the integration of entomology with the general concepts of biology is stressed throughout.

THE EXCRETION OF HONEY-DEW BY *TUBEROLACHNUS SALIGNUS* (GMELIN) (HOMOPTERA : APHIDIDAE)

By T. E. Mittler

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Tuberolachnus salignus (Gmelin) feeding on intact turgid willow stems have a continuous supply of phloem sieve-tube sap forced up the food canal of their stylets by the turgor pressure of their host plant (Mittler, 1957). One may assume, therefore, that the normal ingestion of sieve-tube sap by *T. salignus*, and probably also by other aphid species, is a continuous process which need only be interrupted by the ecdyses. The excretion of honey-dew droplets is, however, a periodic process. Herzig (1937), Smith (1937), Schaefer (1938) and Broadbent (1951) have shown that various environmental factors influence the periodicity with which aphids excrete honey-dew droplets. Herzig (1937) and Schaefer (1938) also noted that the size of these droplets is affected by environmental factors. One must clearly distinguish, therefore, between the periodicity or *frequency of excretion*, which may be defined as the number of honey-dew droplets excreted per hour per aphid, and the *rate of excretion*, which may be defined as the total volume of honey-dew excreted per hour per aphid (Mittler, 1954). It is clear that the rate of excretion is the mathematical product of the frequency of excretion and the droplet volume. Similarly, the rate of feeding may be defined as the volume of sap ingested per hour per aphid. If the total volume of sap ingested by an aphid were excreted by it as honey-dew, its rate of excretion would be equal to the rate of feeding. Schaefer (1938) and Broadbent (1951) pointed out, however, that aphids are liable to lose water by evaporation from their general body surface, and questioned the assumption of Smith (1937) that the frequency of excretion is a reliable measure of the rate of feeding.

The present paper reports on a study of the excretion of honey-dew by *T. salignus* which may throw some light on the effect of various environmental conditions on its feeding activity.

Material and Methods

T. salignus was reared, caged and handled as previously reported (Mittler, 1957, 1958). Two- to four-year-old *Salix acutifolia* Willd. trees, in various stages of development, were used as host plants in the different experiments to be described.

The average frequency of excretion of *T. salignus* in each instar was determined over periods of one to two days by employing the principle of the honey-dew clock devised by Smith (1937). Honey-dew droplets excreted by a colony of aphids were allowed to fall on a strip of kymograph paper moving at a known speed under an aphid colony. The position of each droplet was subsequently detected by heating the paper to caramelise the sugars in the honey-dew, or by spraying it with 0·2 per cent. ninhydrin in butanol to react with the amino-acids in the honey-dew.

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Freshly excreted droplets were collected by means of a glass capillary pipette from a waxed glass plate placed 1 to 2 inches under the colony. The average honey-dew droplet volume and the average rate of excretion were determined for each instar by noting the time and the number of droplets required to fill a 10 or 20 cu. mm. pipette with the honey-dew excreted by a known number of aphids. The data thus obtained also provided a useful check on the frequency of excretion determined by the " honey-dew clock " method.

The total sugar concentration of samples of freshly excreted honey-dew was estimated by the method of Morris (1948). The average live weight was determined by weighing 50 to 100 aphids in each instar.

An estimate of the rate at which *T. salignus* may lose water by evaporation from the general body surface was obtained by confining a colony of aphids in a light-weight, wire-framed muslin cage and weighing the cage hourly.

The effects of changes in temperature on the excretion of honey-dew were observed in the field, the greenhouse and in a cold room. The temperature of the air about an aphid colony was raised by means of an electric radiator.

In order to examine the effects of wind on the excretion of honey-dew by *T. salignus*, aphid colonies were subjected to an air current by means of an electric fan placed several yards away. The wind speed was controlled electrically, and was measured six inches from the aphids by means of an anemometer. The experiments were carried out in a cold room.

Observations on the excretory behaviour of ant-attended *T. salignus* were made in the field and in the greenhouse.

RESULTS

Water loss by evaporation.—Four hundred and eighty-four *T. salignus*, most of which were apterous adults, were found to excrete a weight of honey-dew in one hour equal to 40·4 per cent. of their total body weight. The same aphids confined in a muslin cage for 6·5 hours lost an average of 0·82 per cent. of their body weight per hour to air at 20° C. and 50 per cent. R.H. Under these conditions, therefore, the rate of water loss by evaporation from the general body surface of the aphids is only 2·03 per cent. of the rate at which they excreted honey-dew while feeding normally on their host plant.

The " normal " excretory behaviour.—As *T. salignus* is only occasionally attended by ants, one may assume that its excretory behaviour in the absence of ants is the " normal " one. A few seconds before excreting, nymphal and adult *T. salignus* individuals were observed to raise their abdomen and posterior pair of legs from the willow stem on which they were feeding. When the body was almost at right angles to the stem a droplet of honey-dew was extruded from the anus. Within a second of its appearance the droplet had reached its maximum size and was forcibly propelled from the anus. Neither a nymphal nor an adult *T. salignus* has ever been observed to use one of its legs to propel a honey-dew droplet from the anus. The adult aphid does not possess a well developed cauda with which it could do so in the manner described by Broadbent (1951) for the adults of other " free-living " aphid species. It was not established, however, whether the propulsion of the droplet from the anus of *T. salignus* was entirely due to a sudden constriction of its rectum and abdomen (*see* Weber, 1928), or if it was due to a rapid closure of the anal valves immediately after a droplet had been extruded. As soon as a honey-dew droplet had been excreted the aphid lowered its abdomen against the willow stem.

TABLE I.—*Average droplet volume, frequency and rate of excretion in relation to body weight and instar at 20° C.*

Instar	Frequency of excretion (drops/hr.)	Droplet volume (cu. mm.)	Rate of excretion (cu. mm./hr.)	Live weight of aphids (mg.)	% Ratio of rate to weight
I .	6·9	0·065	0·45	0·34	133
II .	5·4	0·135	0·73	0·84	87
III .	3·9	0·24	0·94	1·79	54
IV .	3·4	0·43	1·43	3·24	44
Apterous adult .	2·2	0·78	1·71	5·14	33

Table I sets out the frequency, rate and droplet volume with which each instar of *T. salignus* excreted honey-dew while subject to continuous illumination from a 100-watt ceiling light in a windowless room at 20° C. The percentage ratio of the volume of honey-dew excreted per hour to the weight of the aphids in each instar is also given. Although instar I nymphs have the highest frequency of excretion, they have the lowest rate of excretion as they excrete the smallest droplets. Whereas instar I nymphs excrete more than their own weight of honey-dew per hour, adult apterous *T. salignus* excrete only 33 per cent. of their body weight per hour. It is interesting to note that Day and Irzykiewicz (1953) calculated from studies with radio-phosphorus that *Myzus persicae* (Sulz.) may hourly ingest an amount of sap equal to 35 per cent. of their body weight. In each succeeding instar the frequency of excretion decreases somewhat but the droplet volume increases almost twofold. Hence the rate of excretion increases with each instar. As it does not, however, increase as rapidly as does their body weight, the ratio of the two decreases markedly with the aphid's development.

At a constant temperature and light intensity the frequency and rate of excretion did not fluctuate appreciably during a 24-hour period. Changes in light intensity did not, however, appear to affect excretion. Adult and nymphal *T. salignus* were found to be able to maintain a steady frequency of excretion for two to three days under constant environmental conditions. During this time the aphids did not change their feeding position on an intact and turgid host plant.

The nymphs did not excrete for five to eight hours during their ecdyses. Excretion commenced almost an hour after the stylets had been inserted into a willow stem. The frequency of excretion of adult apterous aphids was not changed when they gave birth to young.

Neighbouring individuals in a colony of *T. salignus* did not excrete honey-dew droplets in unison. The simultaneous excretion occasionally observed appeared to be a matter of chance.

The effect of temperature.—Table II shows how the excretion of honey-dew by instar III nymphs was affected by temperature. On raising the temperature from 13 to 20° C. the frequency as well as the rate of excretion were almost doubled, whereas the droplet volume remained constant. The increase in temperature also resulted in a slight increase in the total sugar concentration of the honey-dew. When the temperature was lowered from 18 to 12·5° C. the frequency and the rate of excretion were almost halved, whereas the droplet volume remained constant, and the total sugar concentration decreased slightly.

TABLE II.—*Effect of temperature on the excretion of instar III nymphs*

Expt.	Temperature °C.	Exposure time (hours)	Frequency of excretion (drops/hr.)	Droplet volume (cu. mm.)	Rate of excretion (cu. mm./hr.)	Total sugar concn. (% w/v)
1 .	13	3	1·64	0·153	0·25	6·06
	20	2·5	3·02	0·153	0·46	6·37
	25	0·5	3·17	0·145	0·445	6·80
2 .	18	18	3·83	0·184	0·704	3·90
	12·5	2·5	2·00	0·188	0·376	3·73

An increase in temperature from 20 to 25° C. slightly increased the frequency of excretion as well as the total sugar concentration of the honey-dew. The droplet volume and the rate of excretion, however, decreased slightly. As the temperature was increased from 25 to 35° C. the aphids began to raise their abdomens from the stems on which they were feeding, until their bodies were almost at right angles to the stems. The aphids extended their middle and posterior pairs of legs, and supported themselves on their anterior pair of legs and proboscis only, in a "tripod"-like manner. When they had taken up this position the majority of the aphids in a colony extruded and retracted small droplets of honey-dew through their anus at a frequency of 30 to 40 times per minute. This phenomenon was termed "honey-dew-panting". Two to three minutes elapsed before an aphid which had excreted a droplet resumed "honey-dew-panting". Thereafter, the size of the extruded droplets gradually increased until a droplet, many times greater than that finally extruded and retracted, was forcibly extruded and projected from the anus. "Honey-dew-panting" was occasionally observed in the field and in the greenhouse on a warm summer day, particularly if the aphids were directly exposed to sunshine.

The effect of wind.—Marked changes in excretory behaviour were noted when the aphids were exposed to, or shielded from a wind. Thus, when a colony of instar III *T. salignus*, which had regularly been excreting several honey-dew droplets per minute in still air, was suddenly exposed to a steady wind of 1·5 or 2·2 miles per hour, almost 20 minutes elapsed before another droplet was excreted. When excretion was resumed the frequency of excretion was somewhat lower than it was in still air (Table III). The droplet volume, on the other hand, was somewhat greater than in still air. Hence the wind did not reduce the rate of excretion of the aphids as much as their frequency of excretion. The total sugar concentration of the honey-dew excreted by aphids

TABLE III.—*Effect of wind on the excretion of instar III nymphs at* 14° *C.*

Expt.	Wind speed (m.p.h.)	Exposure time (hours)	Frequency of excretion (drops/hr.)	Droplet volume (cu. mm.)	Rate of excretion (cu. mm./hr.)	Total sugar concn. (% w/v)
1	0	2	2·18	0·175	0·38	1·52
	1·5	18	1·78	0·197	0·35	1·61
2	0	2	2·09	0·195	0·407	1·36
	2·2	6	1·74	0·220	0·382	1·45
	0	3	1·95	0·202	0·394	1·38

exposed to wind was slightly greater than that of the honey-dew excreted by them in still air.

Aphids exposed to wind were observed to raise their abdomens from the stem for as long as 20 seconds without excreting. This was done several times during some minutes prior to excreting. Almost half the aphids in a colony excreted within a minute when the wind to which they were exposed was suddenly cut off. Most of the honey-dew droplets excreted during this time were very much smaller than those excreted during continuous exposure to wind or still air. The droplet volume, frequency and rate of excretion normal for still air was, however, rapidly restored.

The effect of ants.—*Lasius niger* L. attended *T. salignus* in the field and in the greenhouse for some weeks early in spring. An ant-attended aphid did not raise its abdomen prior to excreting, nor did it forcibly propel honey-dew droplets from its anus. In response to an ant's solicitations the aphid extruded a honey-dew droplet from its anus, on which it remained poised until the attending ant, or ants, had engorged it. Aphids excreted more frequently when attended by ants than in their absence, but the droplets excreted by the ant-attended aphids were considerably smaller. The " normal " excretory behaviour of the aphids was rapidly restored when the ants were prevented from attending them. These observations confirm those made by Huber (1810) and Herzig (1937) on other aphid species.

DISCUSSION

It may be calculated from the data of Schaefer (1938) that adult *Macrosiphum pisi* (Kalt.) lose an average of 0·84 per cent. of their body weight per hour during starvation. This figure agrees closely with that recorded for *T. salignus*. *M. pisi*, however, appear to excrete a weight of honey-dew per hour which is equal to only 3·14 per cent. of their body weight. This figure is less than one-tenth of that recorded for adult *T. salignus* and for *Myzus persicae* (Sulz.) (Day and Irzykiewicz, 1953).

As feeding aphids probably maintain a high humidity between their bodies and their host plant, one may suppose that the normal water loss by evaporation is only a small fraction of that which is incurred by an aphid during starvation off its host plant. The normal water loss by evaporation is, therefore, probably also only a small fraction of the rate of feeding. Since feeding aphids may, however, have an appreciable water loss when they are exposed to a wind or to a high temperature, their rate of excretion can only provide a reliable measure of their rate of feeding if their water loss by evaporation is determined and taken into account. Broadbent (1951) supposed that the lower frequency of excretion of *Myzus persicae* (Sulz.) in wind than in still air is the indirect result of a greater water loss by evaporation in wind than in still air. The observations on *T. salignus* indicate, however, that the reduction caused by a wind in the frequency of excretion is primarily due to a change in excretory behaviour which wind may affect directly.

The observation that the rate of excretion of honey-dew by *T. salignus* is almost doubled when the temperature is raised from 13 to 20° C., and hardly changes when the temperature is raised from 20 to 25° C. cannot be entirely explained by a higher rate of evaporation at 25° C. than at 20° C. It was previously shown (Mittler, 1957) that at 20° C. the rate of excretion of *T. salignus* was close to the rate at which sap was forced through the aphid's stylets by the turgor pressure of the host plant. One may speculate, therefore, whether at 20° C. the aphid may be ingesting sap at the maximum rate at which its host plant can supply it, so that even if the aphid swallows faster at 25° than at 20° C., it does not ingest more sap. Conversely, at temperatures below 20° C. the aphid may not swallow all the sap with which its host plant could feed it. One may note, however, that Smith (1937) found that the frequency of excretion of continuously feeding instar IV and adult *Hyalopterus pruni* (Geoff.) was almost twice as great at 21·1° C. as at 12·8° C., and again almost twice as great at 29·5° C. as at 21·1° C.

One may also speculate whether the posture assumed by *T. salignus* when exposed to temperatures above 25° C. may enable the aphids to keep cool by allowing air to circulate more freely between their bodies. " Honey-dew-panting " probably results from rhythmical abdominal movements associated with an increased ventilation of the respiratory system. This may also result in a cooling of the aphids.

The results indicate that wind inhibits the excretion of honey-dew by *T. salignus*, and that the aphids are stimulated to excrete when a wind ceases to blow on them. Such a behavioural mechanism may ensure that in nature they do not excrete during gusts of wind which might smother them with their own honey-dew droplets. The fact that the excretory behaviour also changes when the aphids are attended by ants further emphasises the plasticity of the excretory act.

The rectum of a feeding aphid may be regarded as a reservoir into which fluid is continuously flowing and from which fluid is periodically discharged in the form of honey-dew droplets. As the droplets excreted by adult *T. salignus* are considerably larger than those excreted by the nymphal instars, one may suppose that the volume of the droplets excreted by an aphid is determined by its size and, in particular, by the capacity of its rectum. Although the rectum may not normally be fully distended before discharging, an aphid which is subjected to a persistent wind may fill its rectum to its maximum capacity before it " has to " discharge. In contrast an aphid is stimulated to excrete honey-dew droplets when its rectum is probably only partly distended if it is attended by ants or if the inhibition caused by a wind ceases. As the frequency of excretion of the nymphal instars of *T. salignus* is considerably greater than that of the adult aphid, one may also suppose that the rectum of the nymphs is filled relatively more rapidly than that of the adult. The results of Smith (1937) also suggest this to be the case for *Hyalopterus pruni* (Geoff.).

Although the propulsion of a honey-dew droplet from the anus of *T. salignus* appears to be continuous with the extrusion of the droplet, the fact that the ant-attended aphid is able to extrude a droplet without propelling it from the anus suggests that extrusion and propulsion are two separate components of the " normal " excretory act.

SUMMARY

(1) The normal excretion of honey dew by *Tuberolachnus salignus* (Gmelin) is described and the results of quantitative measurements of the honey-dew excreted by the aphid throughout its development are set out.

(2) A distinction is drawn between the *frequency of excretion* and the *rate of excretion.*

(3) The rate of water loss by evaporation from the general body surface of *T. salignus* is relatively small compared to its rate of excretion.

(4) Temperature, wind and ants affect the excretion of honey-dew by *T. salignus* in several different ways.

(5) The excretory mechanism is discussed in the light of the results obtained.

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THE MORPHOLOGY OF THE REPRODUCTIVE SYSTEM OF *PTILINUS PECTINICORNIS* L. WITH A NOTE ON THE TERMINALIA OF THE PUPAL ABDOMEN (COLEOPTERA: ANOBIIDAE)

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Introduction

The internal morphology of the wood-boring beetle *Ptilinus pectinicornis* L. has not been the subject of any previous detailed study. The structures relating to the ovipositor are referred to briefly by Breitsprecher (1928) in his paper on the symbionts found in the Anobiidae, and Sharp and Muir (1912) include a very short account of the aedeagus of the male beetle in their paper on the comparative anatomy of the male genital tube in the Coleoptera. Apart from these references, any previous description of the internal anatomy of *Ptilinus pectinicornis* relates only to the larva.

P. pectinicornis differs from other wood-boring Anobiids in that the imago itself bores into the wood, whereas in other species, apart from the flight-holes made by the young imagines when emerging, boring in the wood is restricted to the larval instars. It seems that in *P. pectinicornis* it is only the female beetle which bores and so it is reasonable to suppose the habit has some connection with egg-laying and that after the hole has been drilled, the eggs would be deposited within it. In fact, it seems that no eggs of this beetle have ever been found, although I have myself seen first-stage larvae in minute galleries radiating from the bore-holes.

Because of this departure from the behaviour usual to the wood-boring Anobiids, it seemed of particular interest to find out if there were also aberrations in the general form of the genitalia as compared with those described in other species (*Anobium punctatum* (Breitsprecher, 1928); *Xestobium rufovillosum* (Fisher, 1937); *Ernobius mollis* (Gardiner, 1953)). Accordingly, the present paper describes the female reproductive organs, associated glands and ovipositor and the male reproductive organs, associated glands and aedeagus. The terminalia of the abdomen of the pupae of both sexes are also described.

MATERIALS AND METHODS

Adult beetles were obtained from an infestation of 2-inch × 2-inch beech posts from The Forest Products Research Laboratory, Princes Risborough. All beetles dissected or otherwise examined had emerged from the wood and were mature. Some of the females had paired and were gravid.

Most of the information was obtained from dissection followed by mounted preparations stained with paracarmine; or by semi-permanent mounts in polyvinyl lacto-phenol-lignin pink. Sections of the ovipositor were made using chloral-hydrate and formol for softening the chitin, according to the method

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recommended by Murray (1937). Preparations of the chitinous portions examined were made using acid-fuchsin for staining after bleaching with diaphenol.

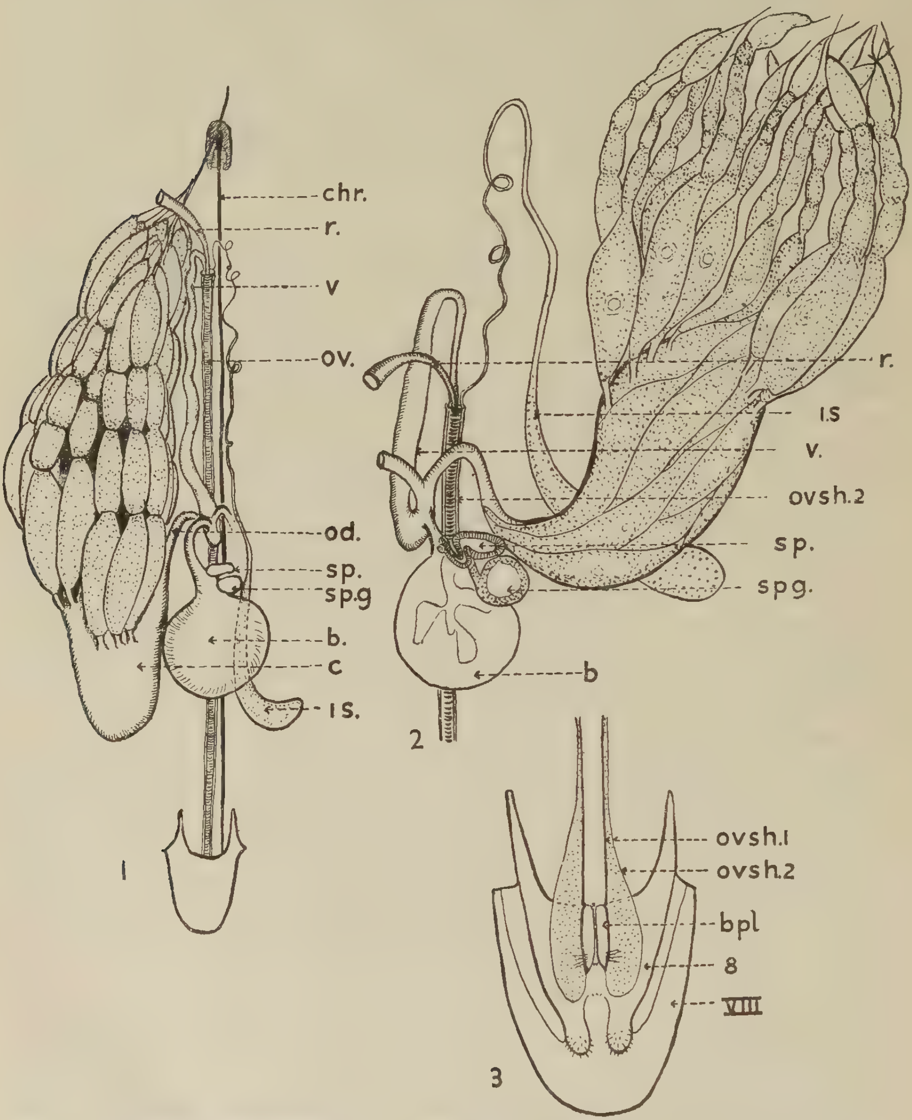
THE FEMALE REPRODUCTIVE SYSTEM

Each ovary consists of 16 ovarioles of the acrotrophic type (fig. 1), each of which is capable of producing at least five eggs ; in the gravid female one fully mature egg and at least four oocytes were seen in relation to each ovariole, and primordia of other egg cells were also visible in the region of the germarium of the egg tube. The egg-laying capacity of the beetle must be controlled largely by time and opportunity, partly owing to its rather leisurely method of boring into the wood for the purpose of oviposition, coupled with a not extensive adult life, and to an apparently very great restriction in type and quality of wood suitable for egg-laying.

The 16 ovarioles are arranged round the highly extensible egg calyx in two rows and their terminal filaments pass anteriorly to the thorax. Each ovariole communicates by a narrow neck with the calyx, which is raised as a dome between the two circles of tubes. Posteriorly, the calyx narrows and in the sixth abdominal segment turns to pass anteriorly as the unmodified oviduct. Thus the calyx when empty, as in the newly emerged female, has the shape of an inverted pear, and the most advanced ovules, still in the ovarioles, are of a discrete oval form. As development proceeds and the female grows gravid these eggs become fusiform and pass into the calyx where they are stored before laying (fig. 2) ; the calyx distends remarkably and stretches back to fill the vacant regions of the posterior abdomen. At least seven eggs are accommodated in each calyx at one time and possibly a greater number may occur, since in all the gravid females dissected the fusiform eggs were still in process of passing into the calyces. It is of interest that in the powder-post beetle *Lyctus brunneus* (Lyctidae) eggs continue to pass into the calyces even if the female remains unfertilized, finally causing the death of the beetle (Altson, 1923). A maximum of 50 eggs in the calyces has been recorded in *L. brunneus* (Parkin, 1934), where the number of ovarioles varies round 12 for each ovary.

In the fourth abdominal segment the oviducts meet in the mid-line to form the vagina. Immediately after the junction the capacious globular bursa copulatrix is evaginated ; it is attached to the vagina by a narrow duct which itself receives the neck of the oval spermatheca. In addition a spherical spermathecal gland occurs posterior to the spermatheca and opening into its duct. The vagina passes forward to the metathorax and here doubles back and, in company with the rectum, enters and traverses the ovipositor. The spiculum ventrale is a long narrow chitinous rod lying parallel and ventral to the ovipositor, which it exceeds in length ; it extends from the anterior part of the metathorax to the pygidium where it is embedded in muscles. It is expanded anteriorly and pointed posteriorly and from the expanded end muscles pass to the basal part of the ovipositor. As in other Anobiid beetles, in Lyctid beetles and others, it is used as a basis for the retraction of the ovipositor into the abdomen after egg-laying. In *Ptilinus* the spiculum resembles in length and form that of *Lyctus* powder-post beetles (Altson, 1924 ; Kojima, 1932) much more closely than that of other Anobiid beetles described (Breitsprecher, Fisher, Gardiner, *l.c.*; Metcalf, 1933).

The ovipositor is of the telescopic type, formed of an inner chitinous cylinder invested by the intersegmental membrane which connects it to the eighth abdominal segment. Oviposition involves the eversion of the structure, the membranous portion becoming the proximal segment of the ovipositor and the chitinous portion the distal. In *Ptilinus pectinicornis* the ovipositor is very



FIGS. 1–3.—*Ptilinus pectinicornis* L. (1) Reproductive system of mature female seen from dorsal side, right ovary removed to expose intersegmental sac ventral to it. (2) Mount of part of reproductive system of gravid female, showing eggs in calyx. (3) Distal portion of ovipositor lying within pygidium. For explanation of lettering see page 64.

long and narrow, when at rest traversing nearly the whole length of the abdomen and metathorax and having a diameter of about 80 μ. The eggs when discharged into the calyx, however, have a diameter more than double this and it is clear that in order to descend the ovipositor they cannot retain their shape but must be greatly squeezed and elongated; it is to be expected that the egg when outside the body would be influenced by the site in which it is laid, for this is the case with *Lyctus* spp. where the ovipositor is inserted into the wood vessels into which the eggs pass in thin gelatinous state before adopting the characteristic cylindrical form (Parkin, *l.c.*).

In *Ptilinus*, the proportions of the ovipositor and form of eggs within the calyces suggest a method of egg-laying similar to that of the *Lyctus* powder-post beetles. As no eggs have been seen after they have been laid it is not known whether they possess the "strand" which is characteristic of the eggs of *Lyctus* spp., and of the Clerid beetle *Tarsostenus univittatus*, a predator on *Lyctus* spp. which also lays its eggs within the wood (St. George, 1924).

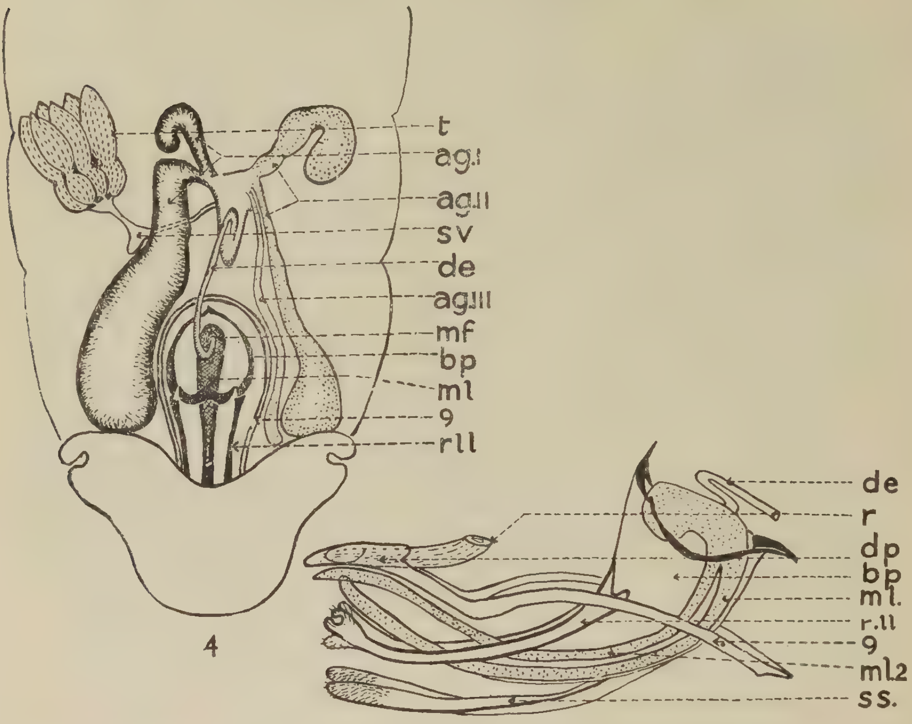
The chitinous inner sheath of the ovipositor terminates in paired basal plates between which lies the gonopore (fig. 3). The anus opens anteriorly to it. These plates lack palps, but are furnished with several groups of chitinous bristles and the whole of the chitinous sheath is covered more or less densely with posteriorly directed hairs. The tip of the ovipositor lies within the pygidial plates, the eighth sternite forming a support for it and terminating in two sensory processes. The membranous sheath of the ovipositor is carried forward in the form of paired intersegmental sacs which then pass posteriorly on either side of the abdomen, enlarging as they go, and ending in the sixth abdominal segment. Such sacs have been described by Breitsprecher (1928) for *Xestobium rufovillosum*, *Anobium striatum* (*punctatum*) and *Sitodrepa panicea*, being replaced in *Ernobius mollis* by specialised hairs in the vagina. Breitsprecher was unable to determine their presence in *Ptilinus pectinicornis* owing to the lack of living material. The intersegmental sacs are continuous with the space between the two ovipositor sheaths. In the region of the pygidium the space is expanded into a wide and flattened pocket in which lies the tip of the chitinous inner sheath of the ovipositor when at rest.

Breitsprecher recognised intersegmental sacs as glandular storage organs for the symbiotic yeasts in the process of their transmission to the mycetomes of the next generation larvae. Examination of transverse sections of the ovipositor shows the chitinous cylinder to be folded concavely along four sides of its length, thus allowing for diametrical expansion during egg-laying. The yeasts, besides filling the intersegmental sacs, can be seen also to occupy a lateral position within the two sheaths of the ovipositor and posteriorly in the pockets of the pygidial region, where their position seems to bear some relation to the bristles on the tips of the basal plates. Possibly small antero-posterior movements of the ovipositor would, with the aid of its bristles and hairs, sweep the yeasts posteriorly in the pygidial pockets from whence it would not be difficult for them to gain entrance to the vagina before egg-laying and so come in contact with the eggs.

THE MALE REPRODUCTIVE SYSTEM

That part of the male reproductive system lying anterior to the genital pocket is covered dorsally by the folded alimentary canal. Removal of the latter exposes the accessory glands, which vary in their degree of development according to the age of the beetle. The testes lie ventral to these glands and on either side of them.

In beetles recently emerged from the wood (fig. 4) each testis can be seen to be composed of six broadly elongate follicles, each somewhat constricted centrally ; they open by short narrow vasa efferentia into the vasa deferentia. In *P. pectinicornis* the vas deferens is modified in shape for the storage of spermatozoa as a seminal vesicle, having a posteriorly projecting dilatation about mid-way along its length. The two vasa deferentia unite medianly in the ductus ejaculatoris which passes dorsally and then posteriorly on its way to the genital pocket.



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Figs. 4–5.—*Ptilinus pectinicornis* L. (4) Male reproductive system seen from dorsal side. Left second and third accessory glands and right first accessory glands and testis have been omitted for the sake of clarity. (5) Genital armature of male seen from right side.

There are three pairs of accessory glands which have the following relationships : at the junction of the two vasa deferentia one pair of glands opens into the genital canal. This pair is opaque white and each member has an anterior and a posterior limb (*a.g.i.*). The second pair is more transparent and each member has a long forwardly directed limb and a long narrow backwardly directed limb (*a.g.ii*). These open into the genital canal at a position more ventral than the first pair. Finally, opening a little posterior to these first two pairs is a third pair of glands ; these are transparent, slender and elongated and lie posteriorly (*a.g.iii*). The precise relationship of these glands one with another would be better determined from newly metamorphosed individuals before the secretions of the glands filled and distended them.

As the beetles become more mature the spermatozoa leave the testes, which degenerate almost completely, and accumulate in the vasa deferentia and its pocket, enormously distending them and adding to the already great confusion of the twisted tubules of the accessory glands.

The ejaculatory duct passes posteriorly and then loops forward and descends into the median foramen of the aedeagus. The aedeagus lies symmetrically in the body (fig. 5). A narrow ring-like sclerite encircles it anteriorly and laterally. Posteriorly this ring expands into a small dorsal plate which covers the anus ; the ring and plate probably represent the ninth abdominal segment.

A very brief account of the aedeagus is given by Sharp and Muir (1912), who describe it as a highly modified example of the trilobe type.

Two peculiarities are noteworthy : from the base of the median lobe (*m.l.*) a second arm arises (*m.l.*2), overlying the median lobe for the whole of the length of the latter and beyond. The median lobe itself is narrow and at its apex it is a little expanded, the median orifice being dorsal and rather wide. The extra arm would provide additional strength for the slender median lobe and would form a covering arrangement for the expanded apex. In the second place the lateral lobes are supported by a sclerite (*ss.*) which arises, according to Sharp and Muir, from the second connecting membrane. This sclerite is bifurcated distally, forming two splayed out arms clothed with minute hairs ; these lie beneath the lateral lobes and presumably help to support them.

THE PUPAE

The two sexes, besides being easily distinguished by the well-known character of the antennae, are also readily separated by the general form of the abdomen. In the female pupa the seventh abdominal segment is about twice the width of the eighth, and a strong ventral prominence posteriorly on the seventh segment is also characteristic.

The developing external genitalia differ only in detail from those of other Anobiid pupae described (Bletchly, 1952 ; Fisher, Gardiner, Metcalfe, *l.c.*).

The female (fig. 6).—The ventral prominence on the seventh sternum before mentioned bears a Y-shaped depression which divides it shallowly into three parts. The eighth sternum has an entire border and the gonopore occurs on a small rounded eminence on the ninth sternum. On either side of the gonopore the sternal plate is produced into paired structures corresponding with the paired palps found in other species. However, in these structures there is no trace of segmentation and they do not develop into the mesocerci which are characteristic of the other species studied ; as has been shown, mesocerci are wanting in *Ptilinus pectinicornis*, the gonopore being bordered by a pair of simple setose plates. The site of the future anus is surrounded by two fleshy plates, the dorsalmost (presumably the ninth tergum) entire and the ventralmost trilobed. The eighth tergum curves postero-ventrally and its swollen curved border encompasses the structures described.

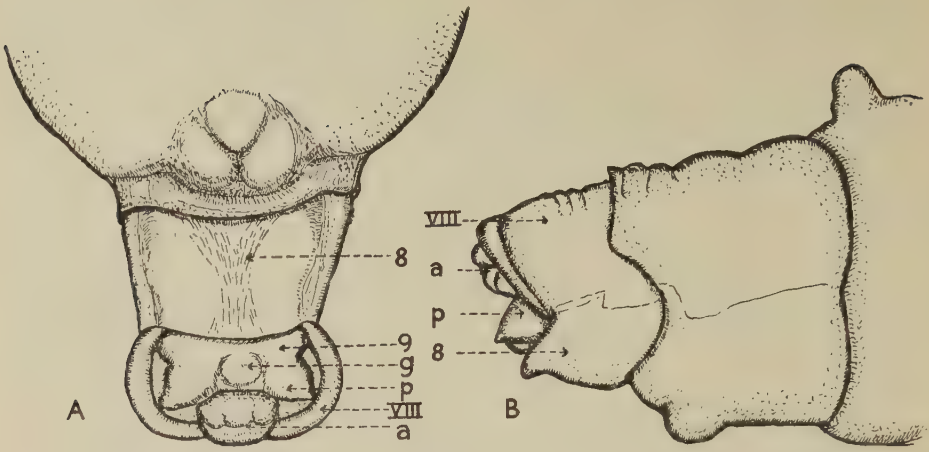

Fig. 6.—*Ptilinus pectinicornis* L. A. Ventral view of posterior segments of abdomen of female pupa. B. Right lateral view of the same.

The male (fig. 7).—A bifid projection on the posterior border of the eighth sternum in the form of two tumid prominences probably represents the developing sclerite associated with the second connecting membrane (Sharp and Muir, *l.c.* and p. 61). These prominences project over the ninth sternite and conceal the origin of the appendages beneath. These consist, as in other species, of the right and left lateral lobes of the future aedeagus and the median lobe bearing the gonopore. These structures arise symmetrically from the ninth sternal plate and have the form of rounded lobes of roughly equal size. The gonopore can be distinguished as a slight depression in the median lobe. There is no asymmetry whatsoever in these appendages, which thus agree with the condition in *Anobium punctatum* (Bletchly, *l.c.*) and disagree with that for *Xestobium rufovillosum* (Fisher, *l.c.*), *Sitodrepa panicea* (Metcalfe, *l.c.*) and *Ernobius mollis* (Gardiner, *l.c.*). Dorsal to the median lobe are two crescentic plates which appear to form the upper and lower margins of the future anus. The eighth tergum curves round ventrally and its swollen posterior border, as in the female, surrounds the genital appendages and anus.

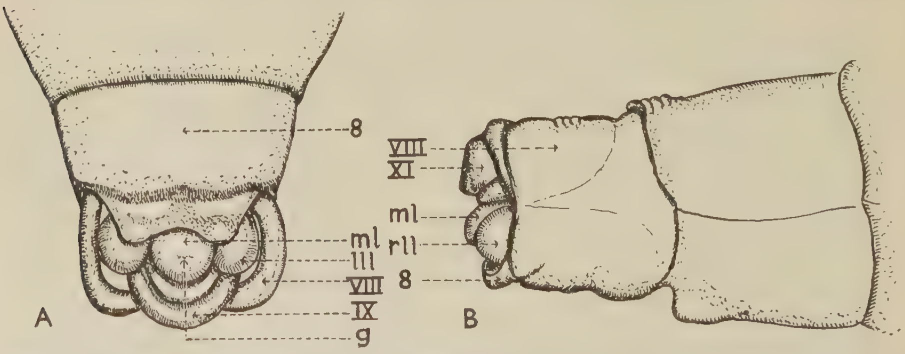

Fig. 7.—*Ptilinus pectinicornis* L. A. Ventral view of posterior segments of abdomen of male pupa. B. Right lateral view of the same.

SUMMARY

A description is given of the female and male reproductive systems of *Ptilinus pectinicornis* L. and a note on the terminalia of the female and male pupae is included.

In detail of form and proportion the female reproductive system shows a greater similarity to that of the *Lyctus* powder-post beetles than to those Anobiid beetles which have been previously described. While the precise method of egg-laying and the appearance of the laid egg is unknown in *P. pectinicornis*, the shape and proportions of the ovipositor and the form of the eggs when within the egg calyx strongly suggest a method of egg-laying within the vessels of the wood similar to that of the *Lyctus* powder-post beetles. Intersegmental glands for the storage of symbiotic yeasts and transmission to the next generation are similar in arrangement to those of the various species of the Anobiidae described, with the exception of *Ernobius mollis*.

The terminalia of the pupae are symmetrical in both sexes, this condition being reflected in the adult ovipositor and aedeagus. The structures described do not differ greatly from those of other members of the Anobiidae.

ACKNOWLEDGMENTS

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Explanation of Lettering

a, anus.
ag.i, left first accessory gland.
ag.ii, right second accessory gland.
ag.iii, right third accessory gland.
b., bursa copulatrix.
bp., basal piece.
bpl., basal plate.
c., calyx.
ch.r., chitinous rod (spiculum ventrale).
de., ductus ejaculatorius.
dp., dorsal plate of ninth abdominal segment.
g., gonopore.
is., intersegmental sac.
l.l.l., left lateral lobe.
mf., median foramen.
ml., median lobe.
ml.2, additional arm of median lobe.
od., oviduct.
ov., ovipositor.
ov.sh.1, inner ovipositor sheath.
ov.sh.2, outer ovipositor sheath.
p., palp.
r., rectum.
r.l.l., right lateral lobe.
sp., spermatheca.
sp.g., spermathecal gland.
ss., supporting sclerites.
sv., left seminal vesicle.
t., left testis.
v., vagina.
8, eighth abdominal sternite.
9, ninth abdominal sternite.
VIII, eighth abdominal tergite.
IX, ninth abdominal tergite.

THE ANTS OF THE GENUS *MYRMICA* IN BRITAIN

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Introduction and Acknowledgments

The various species of the genus *Myrmica* show a diversity of form and colouring even within the comparatively small area of the British Isles. Confusion in nomenclature and the appearance of overlap in some of the commonly used distinguishing characters have combined to make this one of the more difficult groups of species to separate satisfactorily. In this paper the seven British species and their main variations are briefly discussed, and information is given on their distribution and habits.

In assembling the material for this paper the writer has collected widely throughout the British Isles including Ireland, and has also collected or seen material from other European countries. He is indebted to Messrs. M. Bibikoff, W. L. Brown of the Museum of Comparative Zoology, L. Christie, Holger Holgersen of Norway, and many others for the loan of additional specimens, and to their respective authorities for permission to examine various local museum collections including that of the City of Leicester, the National Museum of Wales, the Royal Scottish Museum and the City of Liverpool.

The seven British species comprise *Myrmica rubra* L., *M. ruginodis* Nyl., *M. sulcinodis* Nyl., *M. lobicornis* Nyl., *M. scabrinodis* Nyl., *M. sabuleti* Mein. and *M. schencki* Em. Another species, *M. rugulosa* Nyl. is found in N. Europe including Scandinavia and the Netherlands, and may yet be discovered in E. or SE. England. The nomenclature adopted in the present paper follows Holgersen (1944) in giving specific rank to *M. sabuleti* Mein. and Yarrow (1955) in substituting the name *rubra* L. for *laevinodis* Nylander, and differs in these respects from that employed by Donisthorpe (1927) and by Kloet and Hincks (1945). In addition no status is accorded to supposed interspecific intermediate forms. Forel (1874) erected a series of names to cover these forms which are still widely employed in the literature on *Myrmica*. Brian and Brian (1949) have already shown that apparent intermediates, recognised as such by Donisthorpe, between *rubra* and *ruginodis* were, in fact, clearly assignable to one or other of these species. The frequent occurrence of a mixture of species in *Myrmica* marriage swarms does not in itself provide evidence of interspecific crossing, and among the many hundreds of examples of the British species that have been examined by the writer the few that show abnormal features are clearly assignable to aberrations of one of the species and not to intermediates.

In the following keys, reliance has been placed on easily perceived qualitative differences. Head index measurements are given, however, as additional means of separation between some of the species. These include the frontal index (F.I.), which is the ratio of the minimum width between the frontal ridges and the maximum head width (excluding eyes) × 100, and the scape index (S.I.), which is the ratio of scape length to head width × 100.

Keys to the Males

1 Long curved antennal scapes more than half as long as funiculus; epinota unarmed or with blunt tubercles 2

– Short or angulate scapes half or less the length of funiculus; epinota sharply tuberculate or toothed 4

2 Scape abruptly curved near base; frontal area and petiole striated **sulcinodis** Nylander

– Scape evenly curved; frontal area smooth, petiole not striated . . 3

3 Posterior tibiae and tarsi with long semi-erect hairs; hairs project over upper surface of first femur; antennal segments 4, 5 and 6 scarcely longer than broad; thorax shining black . . . . **rubra** Linnaeus

– Posterior tibiae and tarsi with short semi-decumbent hairs; upper surface of first femur bare; thorax brownish; antennal segments clearly elongate . . . . **ruginodis** Nylander

4 Scape longer than following 5 antennal segments, distinctly angled near base; pale limb and body articulations contrast with dark body colour . . . . **lobicornis** Nylander

– Scape shorter than following 5 antennal segments, more or less bent; colour less contrasted 5

5 Scape as long as first 4–5 following segments; upper surface of first femur bare . . . . **sabuleti** Meinert

– Scape nearly as long as first 3 following segments; upper surface of femur hairy 6

6 Scape thick with long hairs exceeding width; third antennal segment scarcely twice as long as broad; body and legs thickly clothed in long hairs; head not impressed in front of median ocellus **scabrinodis** Nylander

– Scape slender with hairs not exceeding width; third antennal segment more than twice as long as broad; body and legs with short hairs; head impressed in front of median ocellus . . . . . **schencki** Emery

Keys to Queens and Workers

1 Antennal scapes simply curved, not dilated at bend 2

– Antennal scapes angled near base, ridged or dilated at bend . . . 4

2 Scapes abruptly curved near base; frontal area striate; thorax and petiole strongly sulcate; spines convergent . . **sulcinodis** Nylander

– Scape gently curved; frontal area shining; petiole smooth or rugose; worker spines divergent 3

3 Petiole in profile curved or peaked and rounded behind; spines short, space between smooth or very faintly striate; epinotum above usually with transverse striae; postpetiole shining . . . . . **rubra** Linnaeus

– Petiole in profile truncate and angled behind; spines long and coarse, space between with strong transverse striae (exceptionally absent); epinotum above with rest of thorax longitudinally rugose; postpetiole rugose . . . . **ruginodis** Nylander

4 Scape with transverse ridge at bend appearing as tooth in profile . 5

– Scape simple, angled or with flattened extension at bend . . . 6

5 Postpetiole higher than wide in profile; workers with deep meso-epitonal furrow; frons more than quarter head width (F.I. 29·9, range 26–33); scape shorter (S.I. 87·8), ridge at bend appears as fine tooth in profile; smaller dusky species . . . . . . **lobicornis** Nylander

– Postpetiole low and thick; workers with shallow meso-epinotal impression; frons quarter head width (F.I. 25·5, range 24–27); scape longer (S.I. 93); ridge at bend flange-like, less pointed in profile; larger reddish species, rare . . . . **schencki** Emery

6 Scape at bend simply angled, slightly dilated or with short semicircular extension; frons wider (F.I. 38); petiole in profile angled and anteriorly concave; subspinal area about as large as that occupied by postero-lateral epinotal lobes; length of worker 4–4·8 mm. . . . . **scabrinodis** Nylander

– Scape at bend with more or less extensive lateral development, often massive with a longitudinal ridge running forward from the bend; frons narrower (F.I. 34·3); petiole thicker, more rounded in profile; subspinal area larger than that occupied by postero-lateral lobes; length of worker 4·2–5·5 mm. . . . . **sabuleti** Meinert

NOTES ON THE SPECIES

Myrmica rubra Linnaeus, 1758

(Syn. *laevinodis* Nylander, 1846 (Yarrow, 1955))

This species is widely distributed throughout Britain and Ireland but does not range so far north or to such high altitudes as *M. ruginodis.* In N. Britain it is confined to river valleys, as in Oykell, E. Sutherland and in Garve, E. Ross-shire and coastal areas, where it may be abundant as in Galloway (Collingwood, 1953). It is not found on bleak moorland and ascends to 300 m. or more only on limestone pasture, as in the Ingleborough district of NW. Yorks. It is scarce or absent on dry sandy heathland even in S. England and evidently flourishes best in alluvial or moisture retentive soils in sheltered areas. In such places *rubra* may become a dominant species with colonies proliferating freely by nest splitting of queens and workers.

This is one of the more aggressive of the *Myrmica* species and uses its sting freely. Neighbouring colonies will combine to destroy an introduced nest of another species but may also fight among themselves on disturbance. This ant attends both root-feeding aphids and those on the aerial parts of plants, including trees, more consistently than do the other members of the genus. Colonies are normally polygynous with 5–30 or more queens according to the size of the nest, and fresh colonies are usually formed by splitting of the parent nest. Single queens may also found their colonies unaided but seldom do so.

Microgynes sometimes occur. These are queens of normal form but small stature. They occur normally in a form of the allied species *ruginodis,* to be discussed below, but are not known in the writer's experience among the other British species. Tomlin (*in* Donisthorpe, 1927) discovered a microgyne acting as sole queen in a nest at Mathon, Herefordshire. The writer found a colony in a tree stump near Ross-on-Wye in the same county in April, 1953, from which seven microgynes and a number of normal workers were taken. A dealate microgyne was found in September of the same year wandering on the ground near Badsey (Worcs.). These examples measured between 4·3 and 5·0 mm. in length, and at Ross-on-Wye were smaller than the larger workers in the same nest. On the Continent similar microgynes have been recorded by Forel in Switzerland and by Wasmann in Holland (Donisthorpe, 1927), by Sadil (1945) in Czechoslovakia, and by Bibikoff (*personal commun.*) in Switzerland. These occurrences all appear to have been of a sporadic nature, but the tendency for these forms to arise in *rubra* is of special interest in view of their regular occurrence in *ruginodis*.

Intermediate forms between *rubra* and *ruginodis* were widely assumed until the investigations of Brian and Brian (1949) showed that most of these were probably large *rubra* workers. The chief character that has been used to distinguish the species—the relative length of the epinotal spine in the female castes—has been shown to be correlated with head-width. Increasing size of worker as indicated by head-width is usually associated with increasing length of spine, so that the larger *rubra* workers may have the same length of spine as smaller individuals of *ruginodis*. This, accompanied by minor sculpture variations, has sometimes led to confusion between the species, but the more massive flat-topped petiole node of *ruginodis* compared with the peaked or rounded node of *rubra* provides an easily perceived and certain distinction between the species in all cases which have been examined by the writer. Apart from minor variations in sculpture and spine length, *rubra* appears to be one of the more stable of European *Myrmica* and has had fewer named variations than most of the other species.

Myrmica ruginodis Nylander, 1846

(Syn. *rubra* Linnaeus, auctt. (Yarrow, 1955))

This species is ubiquitous throughout Britain. It is present throughout the bleaker moorlands of N. Scotland and is the only ant recorded so far from the Shetlands and St. Kilda, but is equally common in S. Britain. Brian and Brian (1949) discovered this ant to consist of two incompletely dimorphic races, one polygynous with several small queens in each nest, the other monogynous with one large queen. These forms were named by the authors as var. *microgyna* and var. *macrogyna* respectively. In addition to queen size, there are characteristic differences in habitat and behaviour; *macrogyna* is more aggressive, will not normally accept strange queens into its nest, is more generally distributed and predominates in transitory habitats; *microgyna* readily accepts strange queens of its own type and is found in more stable habitats.

In Britain the two races appear to be fairly consistently developed over a large area of W. Scotland, Ireland and NW. England. In other areas the differences do not appear so clearly defined. There is little information from the Continent where *macrogyna* is undoubtedly the commonest form. There are only two references in the literature to small queens known to the writer—a record by Wasmann of a microgynous colony in Feldkirch, Holland (*in* Donisthorpe, 1927) and a reference to the Brians' work by Sadil (1951), in which the author does not comment on the prevalence or otherwise of *microgyna* in Czechoslovakia. This author, however, figures an example of a worker from Sobotka, so presumably this form, although morphologically indistinguishable from *macrogyna* in the worker caste, is to be found there.

Var. *microgyna* is distinctly developed in many areas of Scotland and Ireland especially in west coastal districts. Numerous strong colonies were found, for example, in Kintyre in 1956 along the sea shores. It was of some interest to note the apparent absence of *rubra* from this area, although it had been found in abundance in a previous season in Galloway in similar situations. In the English Lake District *microgyna* was very frequent in *Molinia* tussocks in the mosses (Collingwood and Satchell, 1956). Brian (*personal communication*) reports the discovery of this form in peat bogs in SW. England. These records suggest that *microgyna* tends to flourish in wet cool areas but, according to site distribution evidence from the Lake District and elsewhere, may be replaced by *rubra* in more sheltered places. It is not, however, limited to such areas and has been recorded from a wide variety of habitats including woodland and hillsides.

Throughout its known distribution in Britain *microgyna* is frequently completely sympatric with *macrogyna*. The writer has, for example, found the two forms actually nesting side by side at Allgreave, Cheshire, and in Wharfedale, NW. Yorks. Brian and Brian (1955) give further evidence to show how, by differences in mating behaviour and methods of colony reproduction, the two forms retain their separateness and consequently have some claim to be regarded as true species. The general evidence of incomplete dimorphism provided by the authors themselves, allied to the absence of any reliable means of morphological separation, do not at present justify this suggestion. Moreover, in Midland areas the two forms are frequently difficult to disentangle. One colony found near Matlock, Derbyshire, contained six queens of intermediate size, while another nearby had one. Colonies with three to four queens of intermediate to large size were frequent near Winchcombe, E. Glos., in April, 1956. Polygynous colonies in Scotland frequently contain up to 13 or more queens, but even in these there were considerable differences between the smallest and largest queens. In their original study, Brian and Brian (1949) found that 15 per cent. of the queens obtained from polygynous nests were larger than the smallest *macrogyna* queens. The writer has examined a similar number of examples and found over 34 per cent. in the larger size range and there is evidently a strong tendency to bimodality in this respect in polygynous colonies.

Since the term variety has now no validity in zoological nomenclature, Brian and Brian (1955) have proposed that the two forms *macrogyna* and *microgyna* be designated subspecies. This term is usually restricted to geographic or at least ecological races and cannot, therefore, be properly applied to them, since they can and do frequently occupy the same ecological niches in the same locality throughout their known area of distribution in Britain. The evidence so far available suggests that *microgyna* can scarcely be regarded as a stabilised form but may be an adaptive response of the species towards an oceanic type of climate.

Forel (1874) assumed the existence of forms intermediate between *ruginodis* and *sulcinodis*, to which he gave the name *ruginodis* var. *sulcinodo-ruginodis*. Donisthorpe (1927) attributed to this a variety found on Box Hill, Surrey, in which the workers had a somewhat striate frontal area but were otherwise like *ruginodis*. The writer also attributed certain variations found in N. Scotland (Collingwood, 1951) to this category but on careful re-examination they have proved to be aberrations of *ruginodis*. One worker has the narrow based but strong incurving spines of *sulcinodis* type ; another series of workers have more or less striated frontal areas and both workers and queen are very dark, as in many examples of *sulcinodis*. Nevertheless from their general facies they are quite clearly *ruginodis*. A fine series of large dark workers were sent to the writer by Mr. L. Christie from Loch Droma, E. Ross-shire. Dark colour and stronger sculpturing appear to be normal variations among all the *Myrmica* species found in the Highlands.

Myrmica sulcinodis Nylander, 1846

In Europe this ant is generally restricted to mountain areas but is found in Britain on the lowland heaths of S. England as well as in the Scottish Highlands, where it has been taken up to a height of 600 m. The species is not known from Ireland and there are only two old doubtful records from Wales. It is abundant on well drained gritty moorland both in the Highlands and in similar areas of England from Northumberland to Staffordshire. It has been taken on Dartmoor recently by Dr. M. V. Brian (*personal communication*) and is not uncommon in parts of the New Forest and Dorset heathland as well as in Surrey. In these southern areas nests are often sited in boggy ground and damp tussocks, whereas in N. Britain the species is markedly xerophilous and only found in open ground in well drained areas.

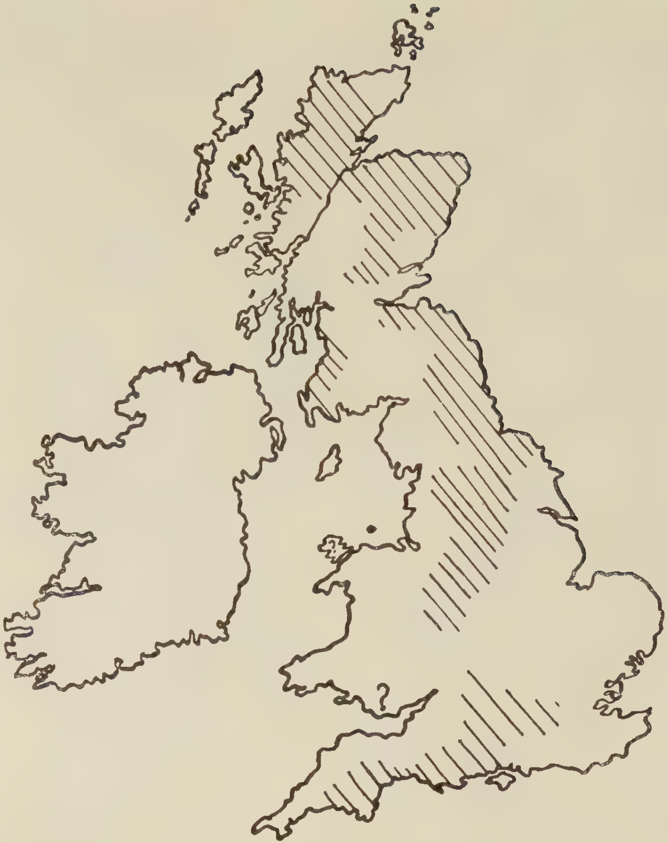
British examples normally show a marked colour contrast between the dark head and gaster and the red thorax. Some Scottish examples would qualify for the dark form described as *nigripes* by Ruszky (1896). Some examples from the French Alps are by contrast much paler than typical British specimens. This distinctive species is very coarsely sculptured. British examples have strong converging spines but in some continental series the spines diverge (Bibikoff collection : Switzerland). Males are readily differentiated from those of *ruginodis* by a more abruptly curved scape and striate frontal area. On the Continent some *scabrinodis* variations with no lobar extension at the bend of the scape are superficially similar, and it is probable that *sulcinodis* var. *sulcinodo-scabrinodis* Forel may refer to such examples. *M. scabrinodis*, however, can always be distinguished by the slight sinuation of the scape at the bend, which in *sulcinodis* is always curved in one plane only.

This is a slow moving but aggressive species preying on other ants and insects and capable of stinging fiercely. Colonies are typically monogynous.

Myrmica scabrinodis Nylander, 1846

This species has almost as wide a range as *ruginodis* in the British Isles and has been taken in almost every county of England, Wales and Ireland and in Scotland from Caithness southwards. It has not been taken higher than about 300 m. in the Scottish Highlands or in Ireland (O'Rourke, 1950) but occurs in a wide diversity of habitat, flourishing in dry sandy areas as well as in woodland and even in boggy ground. Colonies normally arise from single queens but in older nests up to five may be present. In central and south England this species is frequently associated with the ant *Lasius flavus* Fab., occupying a part of the latter's mound nest and preying on the *flavus* workers. In N. Britain it is a component of the loose association of four species including *M. ruginodis macrogyna*, *Leptothorax acervorum* Fab. and *Formica lemani* Bond. studied by Brian and Brian (1951) in W. Scotland which is characteristic for the whole of moorland Britain.

There are considerable variations in sculpture and petiole shape which have led various authors to describe a medley of varieties, subspecies and related



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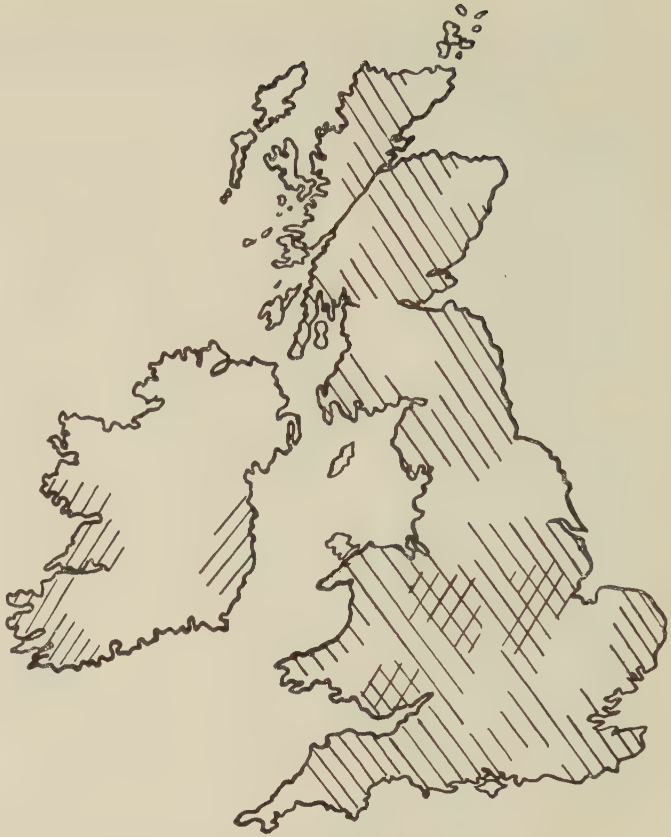

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FIG. 1.—Vice-county distribution of *Myrmica sulcinodis* Nylander (\\\\ ).

FIG. 2.—Vice-county distribution of *Myrmica schencki* Emery (///), and of *Myrmica lobicornis* Nylander (\\\ ).

species. One of the few of interest to British students is the form described by Bondroit as var. *pilosiscapus* which he recognised in specimens from Britain as well as from European mountain areas. Sadil (1951) gives this form full specific status, redescribing it from examples found in mountain areas and peat bogs in Czechoslovakia. This author distinguishes it from *scabrinodis* by the darker colour, deeper sculpture, higher more angled petiole and the presence, in typical examples, of a semicircular extension at the bend of the scape in the female castes ; in the male the petiole is stated to be thicker and more rounded than in *scabrinodis* and has a slight anterior concavity. Many British examples, especially from the Scottish Highlands, would qualify for inclusion in this description. Probably the colony tentatively referred to as var. *scabrinodo-lobicornis* Forel by Donisthorpe (1927) would refer to this form. All the features enumerated above are of the general trend exhibited by *Myrmica* from N. Britain. They are too indistinctly differentiated from the typical form in Britain and too variable even among members of the same nest series to justify separation in the writer's opinion. Named examples from Europe have not been available so that this view can only be regarded as tentative. Sadil's head index measurements, however, fall well within the range he himself gives for *scabrinodis*, while all the differences enumerated are those of degree rather than of kind.

Sadil (1951) has described other *scabrinodis*-like species, including *balcanina* and *slovaca*, both of which have a more or less rectilinear petiole outline from above, approaching that of *rugulosa*. Some of the writer's specimens taken in Worcestershire would approximate to the description of one of these forms but both are, by Sadil's own admission, variable and not consistently different from *scabrinodis*. The males are differentiated by what appear to be small variations in petiole shape. It is not unlikely that one of Sadil's species may be the same as *puerilis* Stärcke (1942) which differs in the male by pilosity characters. Since these authors have concentrated on a different set of diagnostic characters, it is not possible to link their descriptions. According to Wolf's excellent key (1954) to the male castes only of certain West German species *puerilis* is clearly distinguishable from either *scabrinodis* or *rugulosa*.

The variation in scape characters of both *scabrinodis* and *sabuleti* so that there appear to be linking forms has made the distinction between these species more controversial than between other pairs of similar species. Dr. W. L. Brown, in a personal communication to the writer, referred examples of both *scabrinodis* and *sabuleti* sent him from Scotland to the one species *scabrinodis*, stating that in the collections in the Museum of Comparative Zoology the scape characters from most European localities intergraded. In Britain, however, just as Holgersen found in Norway, clear differences in form and behaviour are to be seen wherever the two species occur.

The males are not only distinguished by the size of the scape but also by a consistent difference in pilosity. In *sabuleti* the hairs on the scape and legs are much shorter than in *scabrinodis*. The more massive scape in *sabuleti* females is associated with a narrower frons and the regression lines for frons width on head width in the two species do not overlap. The various differences already indicated in the keys do not appear to vary allometrically and are as apparent in small individuals as in large.

Myrmica sabuleti Meinert, 1860

This species is more localised in its distribution than *scabrinodis* yet ranges as far north as Sutherlandshire. Colonies tend to be grouped together in certain localities in much the same way as *rubra* but are usually monogynous or with few queens. Primary pleometrosis seems to be quite frequent in this species and two or three queens have often been found starting colonies together. This ant appears to flourish best in warm stony places, nesting under stones and seldom or never in tree stumps. In the north it is found only in river valleys, or in coastal districts but is frequent on hillsides in the south, especially in limestone districts.

M. sabuleti tends to be larger, more brightly coloured and somewhat more aggressive than *scabrinodis.* Like *rubra* it will sometimes prey on *Lasius flavus* as on other insects but, unlike *scabrinodis*, is not characteristically associated with this species. In many ways its habits and distribution in Britain resemble those of *rubra*, but its nests are normally sited in drier more insolated places. At the same time it does not seem to tolerate the more arid sandy areas where *scabrinodis* is still capable of flourishing.

Certain forms with deeper sculpture, darker colour and a massive development of the lobar extension of the scape are characteristic of a few localities in the northern Highlands. In some of these specimens the scape is sharply angled and the massive extension appears almost as a tooth in profile. Such examples were mistaken for the rarer and quite different *schencki* by the writer (Collingwood, 1951) and by Donisthorpe, who confirmed the identification at that time. The writer is grateful to Dr. I. H. H. Yarrow for subsequently pointing out the mistake. This form contrasts quite as strikingly with southern examples of *sabuleti* as "*pilosiscapus*" contrasts with southern *scabrinodis*, but can only be regarded as a minor geographic variation.

Finzi (1926) described as the race *lonae* a form described as having a more massive lobar extension than in the type, being at least twice the width of the scape at its narrowest point. Many Highland examples would fit this description and so would numerous series from further south. This appears, therefore, to be a normal variation of the species. A male from the Finzi collection kindly lent by Dr. W. L. Brown, and named by Finzi himself as "*lonae*", does not appear distinguishable from other large *sabuleti* males. In the other direction some nest series have workers with a considerably reduced extension of the scape which, however, is more elongated than in the more extreme forms of *scabrinodis*.

Myrmica lobicornis Nylander, 1846

This species has not been found in Ireland but is widely distributed throughout England, Wales and Scotland from the north coast of Sutherlandshire southward. It is nowhere abundant and colonies are usually single and sparsely scattered over an area. It is a characteristic species of the high Alps and other mountain areas in Europe, but has seldom been found in Britain at higher. altitudes than 300 m. and is less frequent than *sulcinodis* in the Scottish Highlands. *M. lobicornis*, however, appears to be less restricted in habitat than *sulcinodis* and may be found in dry pasture, open woodland and stony hillsides as well as on heaths.

This is one of the easiest species to recognise in Britain. The slender antennal scape bears a small upright process which appears as a small tooth in profile; the body colour is similar to that of *sulcinodis* with the dark head and gaster contrasting with the paler thorax. There is considerable variation in sculpture, spine length and size of antennal tooth even in Britain. The variation in this species over Europe as a whole is more remarkable. In general British examples have a smaller antennal process than seems to be usual among continental material seen. Some Norwegian examples kindly sent by Dr. Holger Holgersen have, by contrast, an outstanding development of the tooth which appears as a wide saucer-like flange larger than that of typical *schencki*.

Myrmica schencki Emery, 1895.

This interesting species is the least common of the British *Myrmica*. Its known distribution in Britain is unlike that of any other ant. It was discovered in one locality in Glamorganshire in 1915 by H. M. Hallett (Donisthorpe, 1927) and it was subsequently found in Ireland in 1926 by A. W. Stelfox (1927). Later discoveries by Stelfox and others (O'Rourke, 1950) have shown it to be widely, though sparsely, distributed there in the SE., and SW., where it has now been taken from about 15 localities mostly in single nests or as individual examples. This species was taken in England for the first time in 1946 by H. E. Hammond and K. G. V. Smith, who collected a single worker from the Shropshire side of the Wyre Forest. Further examples were not found in subsequent visits by the writer and others until April, 1957, when a nest was discovered in the railway cutting not far from the Bridgenorth-Bewdley road in the Worcestershire part of the forest. This nest was revisited in July and a few alatae collected. It has since been discovered in two more localities—a single nest at Barnack in the Soke of Peterborough and a group of a dozen or more nests in a sheltered sand bank by the side of a railway cutting at Wilsford, S. Lincs. Its present known distribution therefore extends in a narrow belt from the East Midlands to the extreme west of Ireland and forms a complete contrast to the north–south distribution of *lobicornis*.

M. schencki is widely distributed through central Europe in lowland areas and on the lower slopes of mountains. It is scarce in S. Scandinavia and, with the exception of *M. rugulosa*, does not extend so far north as the other N. European members of the genus. It is a monogynous species and nests most frequently in the ground in sandy places and not typically under stones as does *sabuleti*. In Ireland O'Rourke (1950) has found it nesting in peat as well as in sandy places and it is not apparently limited to any particular type of habitat there, although it has been found most frequently near the coast.

British examples of this species conform well with those seen from France and Switzerland and, in NW. Europe at least, it is a distinctive and easily recognized species, distinguished by its very narrow frons, large upright process on the scape and very shallow meso-epinotal impression in the worker caste. In S. Europe the species is more variable and in the worker caste sometimes hard to distinguish from the larger forms of *lobicornis*. Males of the two species are, however, quite unmistakable and more unlike than other pairs of similar species already discussed.

SUMMARY

Keys to the males and to the queens and workers of the seven British species of *Myrmica* are given. Their distribution, habits and main variations in Britain are briefly discussed.

The vice-county distributions of *M. sulcinodis* Nyl., *M. lobicornis* Nylander and *M. schencki* Emery are mapped.

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DIPTERA-CYCLORRHAPHA FROM GOUGH ISLAND, SOUTH ATLANTIC

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The collections made by the Gough Island Scientific Survey, 1955–56 include a dozen species of cyclorrhaphous Diptera, which are identified in this paper. The few nematocerous Diptera will be recorded elsewhere ; there are no Brachycera. The identification of the Cyclorrhapha is greatly facilitated by the paper by Frey (1954), which describes the collection made in Tristan da Cunha by the Norwegian Expedition of 1937–38. The British Expedition collected fewer species than the Norwegians, but much longer series of each. The most significant fact that emerges from the present collection is that Gough, though 230 miles from Tristan, seems to be faunistically just another of the Tristan group.

Frey arranged the flies he recorded from Tristan into three categories : endemics ; species of world-wide, or at least very extensive distribution ; and synanthropes, or species brought to the islands by man. The 12 species in the present collection can be arranged similarly :

Endemics
*_Parascaptomyza altissima_
*_Tristanomyia frustulifera_
Dimoecenia tristanensis

World-wide
†_Ornithomyia remota_
Limosina plumosula
Thoracochaeta zosterae
Meoneura sp.
Megaselia sp.
*_Fucellia maritima_

Synanthropes
*_Fannia canicularis_
Calliphora vomitoria
*_Lucilia sericata_

Those marked (*) are in Frey's list from Tristan. _Ornithomyia remota_ (†) was once thought to be endemic, but according to Bequaert it is synonymous with a South American species.

Having regard, not only to the remoteness of Gough Island, but also to the steepness and roughness of its coastline, as described by Heaney and Holdgate, it is difficult to imagine how the faunal interchange with the islands of the Tristan group can have taken place. This is particularly true of the winged, but flightless Drosophilid, _Tristanomyia._ As for the " synanthropes ", the account of Gough Island and its previous explorations makes it seem surprising that so few visitors, landing with so much difficulty, could have taken with them so many Palaearctic flies.

The detailed localities are quoted as given on the labels, and can be understood by reference to Heaney and Holdgate's paper, with its excellent map. As far as the Cyclorrhapha are concerned the detailed localities do not seem to be significant, and it is likely that flies occur all over the island where there is suitable debris.

PROC. R. ENT. SOC. LOND. (A) 33. PTS. 4–6. (JUNE, 1958).

DROSOPHILIDAE

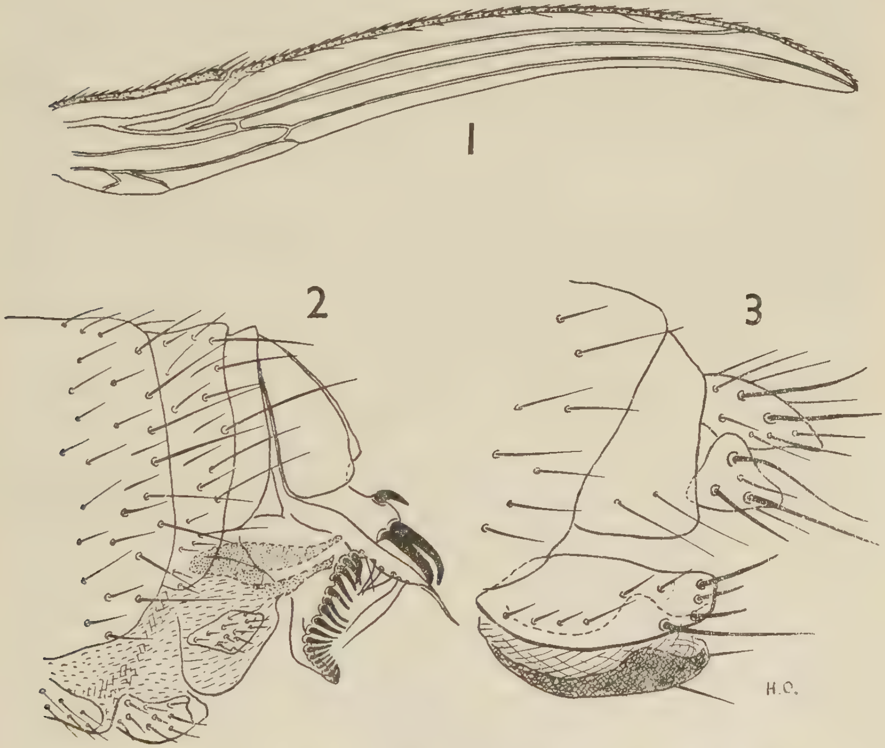
Parascaptomyza (*Macroscaptomyza*) *altissima* Frey, 1954, *Norw. sci. Exped. Tristan da Cunha* **26** : 27

74 specimens. A 19. Mixed vegetation by cliff foot, alt. 10 ft., 6.i.56 ; A 18. Around hut, Base, The Glen, alt. 20 ft., 6.i.56 ; A 17. Light trap at Base, The Glen, 23.xii.55 ; A 29. Upland *Blechnum-Apium-Scirpus* Zone, Gonydale Camp. alt. 1500 ft., 26.i.56 ; A 38. Tussock grass, Penguin Island ; A 7, B 17. 1 spirit specimen off *Diomedea chlororhynchus*, Glen Beach, 19.iv.56.

Frey described this species for the first time from Tristan, and recorded it from all three islands, Tristan, Nightingale and Inaccessible. He remarked on its similarity to *Drosophila funebris*.

Tristanomyia frustulifera Frey, 1954, *Norw. sci. Exped. Tristan da Cunha* **26** : 31

4 ♂, 8 ♀. From *Histiopteris* association. The Glen, alt. 30 ft., 30.xi.55 ; A 19. Mixed vegetation by cliff foot, alt. 10 ft., 6.i.56 ; A 18. Around hut, Base, The Glen, alt. 20 ft., 6.i.56 ; A 16. Tussocks in penguin rookery, The Glen, alt. 50 ft., 26.xii.55 ; A 7, A 8 ; Misc.



FIGS. 1–3.—*Tristanomyia frustulifera* Frey : (1) right wing ; (2) male genitalia ; (3) female genitalia.

This fly is remarkable for the narrow-strap-like wing, and since Frey described it from a single male, it remained doubtful whether this character might not be confined to one sex. The present material contains several specimens of each sex, and shows that the wing-structure is the same in both. As will be seen in figure 1, in spite of the deformation of the wing it still retains the complete venation of the Drosophilidae.

The wings and halteres of this fly are very much like those of *Amalopteryx maritima* Eaton, 1875, described from Kerguelen Is., and later figured by Enderlein (1903, *Wiss. Erg. Deutsch. Tiefsee Exp.* **3**(7), plate XXXV, figs. 58, 62). Enderlein put *Amalopteryx* in the Ephydridae, and examination of the type material of this fly in the British Museum shows that it is unmistakeably an Ephydrid. The shape of the wing in the two genera is a remarkable convergence.

The differences in genitalia between the two sexes are shown in figures 2 and 3, and even in a dried specimen it is usually possible to recognize the female by the large *ventral* lamellae (fig. 3). These are large and heavily sclerotised, and their appearance recalls the acanthophorites of certain Asilidae, which are used for ovipositing in sand or loose soil.

EPHYDRIDAE

Dimoecenia tristanensis, Frey 1954, *Norweg. sci. Exped. Tristan da Cunha* **26** : 38.

63 specimens. A 18. Around hut, Base, The Glen, alt. 20 ft., 6.i.56 ; A 1. From *Histiopteris* association, alt. 30 ft., The Glen, 30.xi.55 ; A 17. Light trap, Base, The Glen, 23.xii.55 ; A 9. From banks and boulders by stream, The Glen, alt. 250 ft., 7.xii.55 ; A 19. Mixed vegetation by cliff foot, alt. 10 ft., 6.i.56 ; A 34. From hut, stream and beach debris in The Glen, alt. 20 ft., 30.i.56.

Frey points out that the genus *Dimoecenia* has hitherto been recorded only from the New World. It is very close to *Ephydra*, and was originally described from Nearctic material, but Cresson later included species from Argentina and Chile, so that the occurrence of a species of this genus in Tristan and Gough might be a pointer to a fauna of Gondwanaland origin.

HIPPOBOSCIDAE

Ornithomyia remota Walker, 1849, *List. Dipt. Brit. Mus.* **4** : 1144

8 pinned specimens. A 18. Around hut, Base, The Glen, alt. 20 ft., 6.i.56 ; A 19. Upland *Blechnum-Apium-Scirpus* zone, Gonydale Camp, alt. 1500 ft., 26.i.56 ; 30 specimens in spirit, mostly from *Rowettia goughensis*, Little Beach, 29.xii.55 ; some from *Porphyriomis comeri*, Glen rookery, 25.iv.56.

This is the only Hippoboscid known from either Gough or Tristan. At one time Austen considered that it was a synonym of *O. avicularia* L., a species of wide distribution, but he afterwards altered his opinion. Bequaert (*in* Frey, 1954) says that *O. remota* is not separable from a species that is found in Chile and Argentine, so giving another hint of Gondwanaland affinities.

BORBORIDAE

The two species recorded from Tristan by Frey (1954) are both distinctive, and neither was taken on Gough by the present expedition. Instead were taken two Palaearctic species of wide distribution, the second of which is common on beaches in the British Isles.

Limosina plumosula Rondani, 1880, *Bull. Soc. ent. Ital.* **12** : 29 ; Richards, 1930, *Proc. zool. Soc. Lond.* **18** : 299.

12 specimens. A 18. Around hut, Base, The Glen, alt. 20 ft., 6.i.56 ; A 19. Mixed vegetation by cliff foot, alt. 10 ft., 6.i.56 ; A 36. Light trap at base, alt. 20 ft., 1.ii.56.

Thoracochaeta zosterae Haliday, 1833, *Ent. Mag.* **1** : 178.

(*Limosina*) 1 specimen. A 28. Penguin rookery in small cave, Sophora Glen, 22.i.56.

Carnidae

Meoneura sp.

1 ♀. A 28. Penguin rookery in small cave, Sophora Glen, 22.i.56.

The reddish-yellow areas of the frons and face are present as in the British *M. flavifacies* Collin, but the Gough Island specimen is bigger and more robust. These flies have been bred from carrion and from the debris in old birds' nests, and there must be a great many undescribed species throughout the world. The male genitalia are distinctive, and enable the British species, at any rate, to be readily separated (Collin, 1930, *Ent. mon. Mag.* **66** : 82–89), but a single female from a remote island cannot be identified.

Phoridae

Megaselis sp.

2 ♀ from locality B 15–16. The same remarks apply to these as to the *Meoneura* above.

Muscidae

Fannia canicularis Linnaeus, 1761, *Fauna Suec.* Ed. II : 454.

11 specimens. A 18. Around hut, Base, The Glen, alt. 20 ft., 6.i.56 ; A 29. Upland *Blechnum-Apium-Scirpus* zone, Gonydale Camp, alt. 1500 ft., 26.i.56.

The Lesser Housefly was also recorded from Tristan by Frey (1954).

Fucellia maritima[1] Haliday, 1838, *Ann. nat. Hist.* **1**(2) : 186

32 specimens. A 19. Mixed vegetation by cliff foot, alt. 10 ft., 6.i.56 ; A 34. From hut, stream and beach debris in Glen, alt. 20 ft., 30.i.56 ; A 17. Light trap at Base, The Glen, alt. 20 ft., 23.xii.55 ; and a number labelled simply " Base ".

This maritime littoral species is common on the beaches of the British Isles, along with *Thoracochaeta zosterae.*

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[1] Dr. van Emden tells me that, in his opinion, all the *Fucellia* from Gough, as well as those from Tristan, belong to *intermedia* Lundbeck, which has at various times been merged with *maritima* : see Collin, 1931, *Ann. Mag. nat. Hist* (10) **7** : 88. He also refers the two female *Calliphora* to *croceipalpis* Jaennicke (*antarctica* Schiner), a southern form which Senior-White (1940, *Fauna Brit. India Dipt.* 6, Calliphoridae : 40) merges with *vomitoria.* This does not affect the ecological discussion.

CALLIPHORIDAE

Calliphora vomitoria Linnaeus, 1758, *Syst. nat.* (ed. x) **1** : 595

2 ♀. A 18. Around hut, Base, The Glen, alt. 20 ft., 6.i.56 ; B 17.

Lucilia sericata Meigen, 1826, *Syst. Beschr.* **5** : 53

15 specimens. A 19. Mixed vegetation by cliff foot, alt. 10 ft., 6.i.56 ; A 20 ; " Base ".

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THE ROOT-PIERCING SPIRACLES OF THE LARVA OF *CHRYSOGASTER HIRTELLA* LOEW (DIPTERA : SYRPHIDAE)

By J. C. Hartley

(*Department of Zoology, University of Bristol*)

Introduction

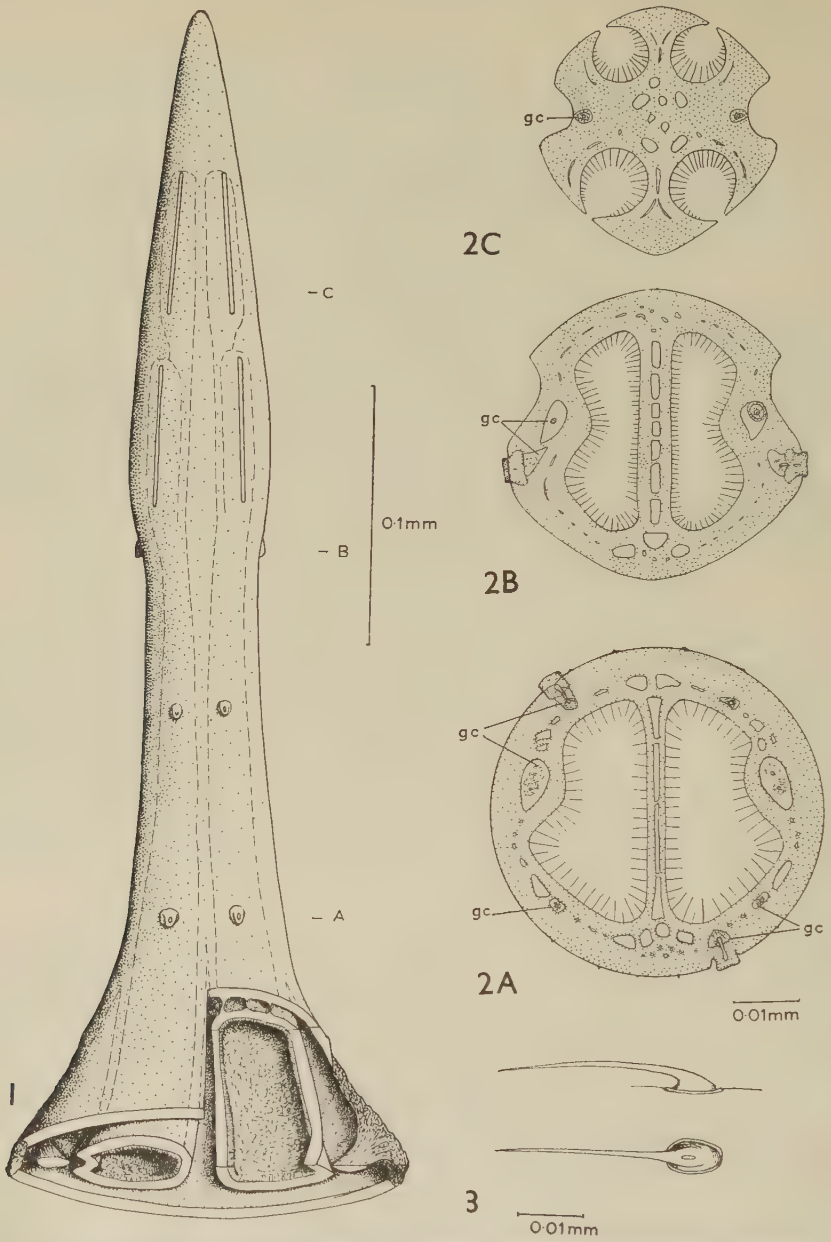
The larva of *Chrysogaster hirtella* Loew has the spiracles of the eighth abdominal segment so modified that it is able to obtain oxygen from the intercellular air spaces in roots and stems of certain aquatic plants. The spiracles of only a few larvae are so modified. A list of these is given by Hinton (1953). The modified spiracles of *C. hirtella* have previously been described by Varley (1937), who has mistaken the dorsal side for the ventral and has omitted from his description the more interesting structures of these spiracles.

The Postabdominal Spiracles of the Third Instar

The postabdominal spiracles are fused together, as in the great majority of the Syrphidae. They are borne on the end of a telescopic breathing-tube, which is an extension of the eighth abdominal segment. The paired tracheal trunks in this tube join the felt chambers at the base of the fused spiracles and are not constricted before so doing. The fused posterior spiracles are about 0·75 mm. long and consist of two distinct parts, a distal part 0·4 mm. long which forms the piercing stylet, and a basal part 0·3 mm. long, which is much wider and which contains the greater part of the felt chamber and the stigmatic scars. The fused spiracles taper rapidly to form the piercing part just beyond the stigmatic scars.

The cuticle of the piercing part is thick and heavily sclerotised. Transverse sections of its basal half appear as illustrated in figure 2, which shows the two large canals which are the extensions of the felt chambers, and around these numerous smaller canals. The spiracular slits are borne on the spear-like end, one pair only dorsally, but two pairs ventrally one behind the other. The dorsal slits are 0·08 mm. long and 0·0025 mm. wide, and the ventral each about 0·06 mm. long. Each slit opens into a cylindrical chamber immediately beneath and these chambers join with extensions of the felt chambers just basal to the spear-like end of the spiracles. The distal ventral slit chamber connects with the felt chamber through the proximal slit chamber. On the outside of the spear-like end there are two longitudinal, laterally placed, grooves.

The perispiracular glands are situated around the felt chambers in the wide part of the spiracles. The ducts from them run to their openings along some of the smaller canals (fig. 2, *gc*), the function of the rest of which is not known. They appear to be constant in number. All the smaller canals communicate with the haemocoele. The openings of the perispiracular glands of which there are four pairs, two ventral, one dorsal and one lateral, are on the tubercles that have been previously referred to as sensilla. The lateral openings are double, as is usual in



FIGS. 1–3.—*Chrysogaster hirtella* Loew. (1) Ventral view of distal part of postabdominal spiracles of third instar larva cut to show the commencement of the canals, the upper part of the felt chamber, and the stigmatic scar. (Sections through points *A*, *B* and *C* are shown in figure 2.)

(2) Sections through postabdominal spiracles, *A*, *B* and *C* corresponding to the positions shown in figure 1. The felt lining is shown diagrammatically. The positions of the perispiracular gland openings are not always quite symmetrical, hence the apparent asymmetry of *A*. *gc*, perispiracular gland canals.

(3) Tubercle of perispiracular gland opening with undamaged spine.

the Syrphidae, one part opening on a tubercle and the other along the groove on the spear-like end of the spiracles. Before the old cuticle has been shed, a simple spine arises from each of the tubercles on the newly formed spiracles, and points towards their base (fig. 3). It usually appears to be broken off near its base when the old cuticle is shed ; if not it would certainly be broken when the spiracle is used for piercing roots. In their undamaged condition these spines are somewhat similar to those shown by Bhatia (1939) for *Syrphus luniger* and by Heiss (1938) for *Epistrophe* and *Pipiza*.

The spiracles of the third instar are formed within the breathing tube of the second instar (fig. 4), during which time this breathing tube is kept extended. The tip of the new spiracle lies just basal to the felt chamber of the previous instar. The tracheal system of the second instar is pulled out through the sides of the third instar spiracles, which places the scars in a very unusual position, causing them to be outside (anterior) the spiracle, whereas the normal position in Diptera is on the inside (posterior) of the spiracles, with the spiracular plate more or less enclosing them. Scars in this position in *C. hirtella* would prevent the formation of a fine piercing stylet. Their transposition has resulted in the scar strand running through the felt chamber from the inner lateral side to the outer lateral side, so that the felt chamber has been interrupted across the middle by a bridge carrying the scar strand. This is bypassed by a dorsal and a ventral passage which reunite before entering the piercing part of the spiracles (fig. 5). The scar strands are comparatively stout ; they probably serve as supporting struts analogous to the tracheal anchors described by Hinton (1955) in some Tipulidae.

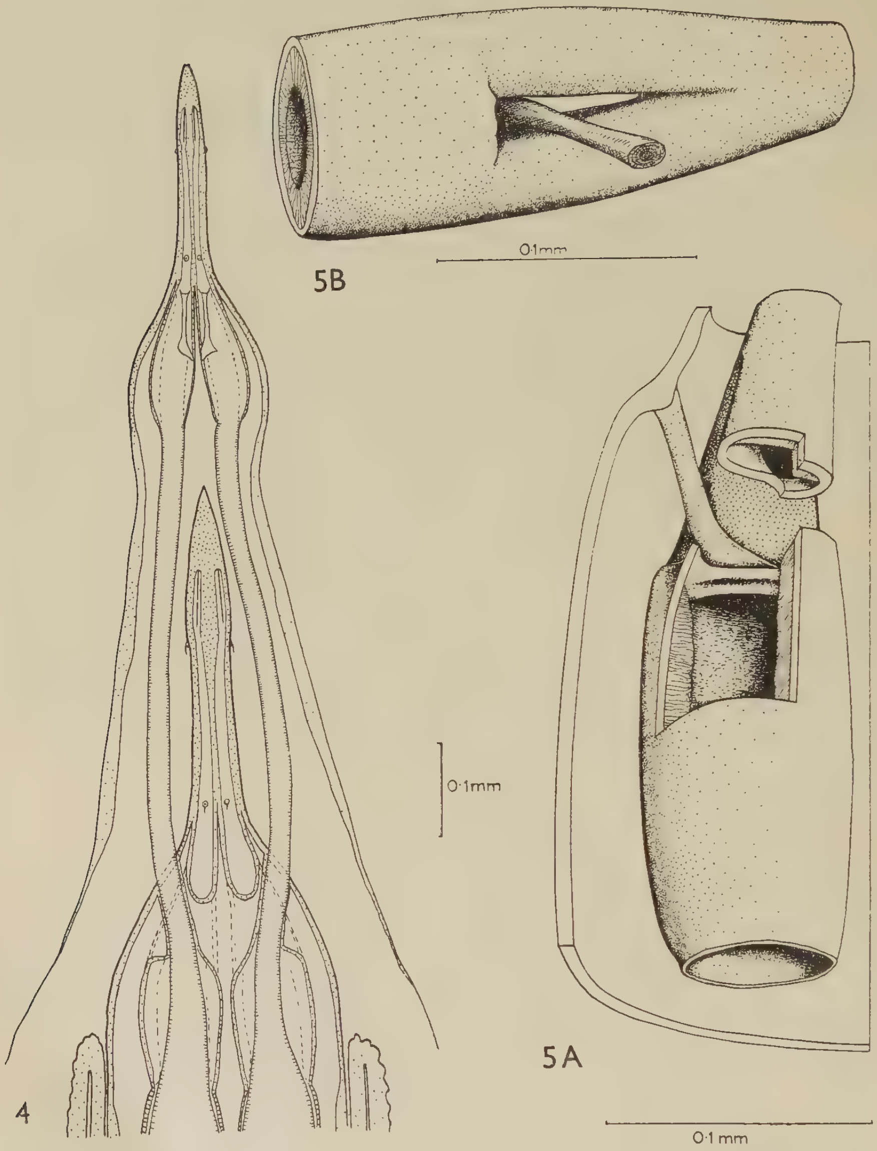
Around the basal part of the felt chamber is a thick felt which extends to the point where the stigmatic scar strands arise. Beyond this it becomes shorter and very fine. The inner stigmatic scar is without felt. At no point does the felt occlude more than one-third of the felt chamber.

THE POSTABDOMINAL SPIRACLES OF THE SECOND INSTAR

The general shape of the second instar spiracles (fig. 6) is much the same as in the third instar. There are only two pairs of slits, one dorsal and the other ventral ; they are much smaller, being 0·025 mm. long and less than 0·002 mm. wide. The total length of the spiracles is 0·42 mm. The scar strands run out dorsally near the mid-line ; they leave the felt chambers on the inner dorsal sides, and are thus in a more typical position. The felt chambers are not interrupted by them. The other details are the same as the third instar.

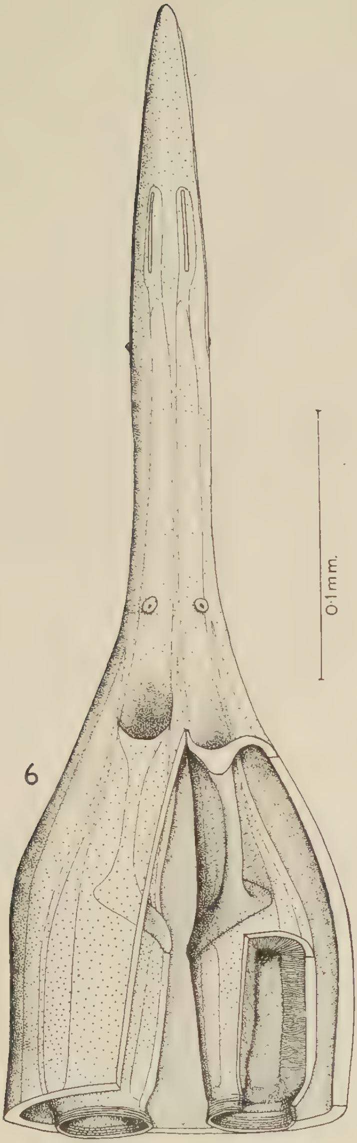
THE POSTABDOMINAL SPIRACLES OF OTHER SPECIES OF *Chrysogaster*

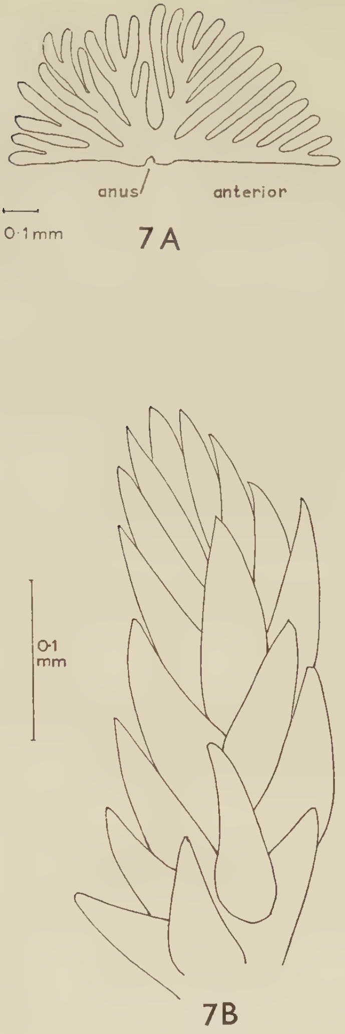
Chrysogaster solstitialis Fall. is found in similar habitats to *C. hirtella.* It does not, however, obtain its oxygen from a plant but directly from the surface. The postabdominal spiracles are borne on the end of a longer telescopic breathing tube. The fused spiracles have a cylindrical base about 0·2 mm. long and a hemispherical cap (fig. 8) which carries three pairs of spiracular slits, the peri-spiracular gland openings, and the stigmatic scars. The latter are central and hence in the typical position. There are eight pectinate setae around the base of the spiracular cap ; they are hydrophobic and help to support the spiracles on the surface of the water. There is no clear distinction externally between the



Figs. 4–5.—*Chrysogaster hirtella* Loew. (4) Semidiagrammatic optical section from above of third instar spiracles within second instar breathing tube during the moult. The apparent discontinuity of the felt chambers is caused by the bridge carrying the second instar tracheae. The third instar felt chambers pass above and below the bridges.

(5) Basal part of third instar felt chamber. (A) Dorsal view with upper part of divided chamber cut away to show the scar strand. Lower part of the divided chamber is shown intact beneath. (B) Lateral view showing the two chambers with the scar strand between them.





FIGS. 6–7.—*Chrysogaster hirtella* Loew. (6) Dorsal view of fused postabdominal spiracles of second instar larva, with a part cut away to show a scar strand. A felt chamber is also partly opened.

(7) Anal papillae. (A) Diagrammatic representation of the right half of the anal papillae in the extruded position. (B) Detail of one of the branchlets showing the covering of smaller papillae.

spiracles and the breathing tube, the distal part of the latter being as heavily sclerotised as the spiracles. Internally the transition from felt chamber to trachea is quite distinct. The whole posterior respiratory structure generally resembles that of *Eristalis*.

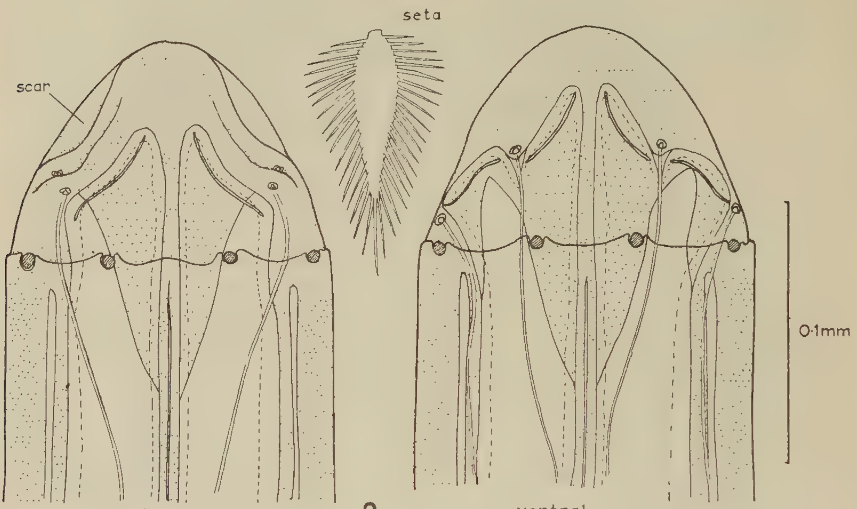


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Fig. 8.—*Chrysogaster solstitialis* Fall. Fused posterior spiracles. The setae have been removed and their positions shown by the shaded circles. One of the setae is shown separately.

Chrysogaster (*Liogaster*) *metalina* Fabr. and *C.* (*Orthoneura*) *splendens* Meig. have posterior respiratory structures that are very similar to *C. solstitialis.* They are also found in similar habitats.

General Notes

The larvae of the genus *Chrysogaster* live in rich organic mud around pools and streams. Most of the species obtain air directly from the surface by telescopic breathing tubes bearing the spiracles. *C. hirtella* is also able to obtain air from the roots and stems of waterside plants by means of its specially modified spiracles. Varley has recorded it using *Glyceria maxima* (= *aquatica*); the present writer has found the larvae associated with *G. fluitans* and various other semi-aquatic plants. Apart from the postabdominal respiratory apparatus, these larvae are all very similar. They are all metapneustic even in the third instar. The anal papillae, which have been used by Gäbler (1930) for distinguishing some of the species of *Eristalis*, are very complex, and probably cannot be used conveniently in this genus, as in their general appearance they are very similar. They are much branched, there being about 48 terminal branchlets in *C. hirtella* (fig. 7) and each is further covered with numerous smaller papillae.

Acknowledgment

I wish to thank Dr. H. E. Hinton for his help in producing this paper.

SUMMARY

1. The root-piercing spiracles of the third instar larva of *C. hirtella* are described and illustrated.

2. Attention is drawn to the curious positioning of the stigmatic scar strands in the felt chambers ; it is suggested that the scar strands also function as supporting struts comparable with tracheal anchors.

3. The spiracles of the second instar larva are compared with those of the third instar.

4. A general comparison with other species of the genus is made.

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NOTES ON THE BREEDING HABITS OF SOME CULICINE MOSQUITOES (DIPTERA : CULICIDAE) IN SOUTHERN GHANA

By G. Surtees

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During 1956 a survey was carried out at Tafo in southern Ghana to collect data on the breeding habits of biting flies. Tafo is 70 miles north of Accra and 600 feet above sea level, whilst the surrounding hills rise to some 2000 feet. This region has 50–60 inches of rain per year and a dry season extending from November to March; the survey was carried out during the rains. Tafo is situated in the main cocoa growing area of Ghana and the locality surveyed belonged to the West African Cocoa Research Institute. For the purpose of surveying it was divided into (*a*) the main cocoa growing area, (*b*) an area alongside the reservoir, (*c*) two residential areas.

Attention was mainly focused on the Culicidae, and as a result of this work the following observations can be made. A list of the types of breeding sites found is given below.

(1) *Plant Axils*

Musa sapientium.
Ananas comosus.
Xanthosoma sagittifolium.
Heliconia sp.

(2) *Natural Sites*

Rolled leaves.
Cocoa husks.
Tree holes.
Snail shells.
Rock pools.
Ground pools.
Crab holes.

(3) *Domestic Vessels* (e.g. *Native Pots*)

The empty snail shells (*Achatina* sp.) and cocoa husks when filled with water made excellent breeding places for several mosquito species. In all 1410 potential breeding sites were tested, 24·7 per cent. were positive for culicine species and of this total 25·7 per cent. were found in the cocoa plantation, 35·9 per cent. along the reservoir edge, 33·5 per cent. in the residential areas and 4·9 per cent. elsewhere. The species taken were as follows.

Eretmapodites chrysogaster Graham.
E. pencillatus Edwards.
E. grahami Edwards.
E. oedipodius Graham.
E. sylvestris Ingram and de Meillon.
E. quinquevittatus Theobald.
Culex (*Culiciomyia*) *nebulosus* Theobald.
C. (*Culex*) *ingrami* Edwards.
C. (*Culex*) *annulioris* Theobald.
C. (*Culex*) *perfidiosus* Theobald.
C. (*Neoculex*) *rima* Theobald.
Aedes (*Stegomyia*) *simpsoni* Theobald.
A. (*Stegomyia*) *apicoargenteus* Theobald.
A. (*Stegomyia*) *aegypti* Linnaeus.
Harpagomyia taeniarostris Theobald.
Uranotaenia ornata Theobald.
U. fusca Theobald.
U. annulata Theobald.
U. candidipes Edwards.

PROC. R. ENT. SOC. LOND. (A) 33. PTS. 4–6. (JUNE, 1958).

ECOLOGICAL DISTRIBUTION OF SPECIES

Eretmapodites chrysogaster

Haddow (1946) recorded this species from leaf pools and leaf axils in a forest region in Uganda, and Hopkins (1936) quoted it as being found in old tins, tree holes, bamboo stumps and water tubs. Kerr (1933) pointed out that this species was common in all cocoa growing areas.

In this investigation *E. chrysogaster* was the most common culicine species breeding in the cocoa plantation and larvae were abundant in rolled leaves and rotting cocoa husks on the plantation floor. The numbers recorded in each breeding site indicated that the species had a distinct preference for the cocoa husk type of breeding site. This would support previous evidence that the species is to be found breeding in water which is rich in decaying vegetable matter. It was also taken from the flower heads of *Heliconia*, from snail shells and from banana leaf axils but in no great abundance. Along the reservoir edge it was taken in small numbers from rolled leaves and also from a tree hole. In the residential area it was recorded once in a rolled leaf.

E. pencillatus

Haddow (1946) found this species in the empty shells of *Achatina* sp. and in this survey it was recorded five times, on three of these occasions from the empty snail shells. It was not found outside the cocoa plantation.

E. grahami

This species was only recorded twice, once from a rolled leaf in the cocoa plantation, which corresponds to its typical breeding site, and once from a ground pool near to a small stream.

E. oedipodius

The *oedipodius* group of mosquitoes have been recorded as larvae from leaf pools (Haddow, 1946), and Hopkins (1936) gave the breeding site as " large fallen leaves in the forest ". During these studies *E. oedipodius* was mainly taken from rolled leaves in the cocoa. Here also it was taken once from a snail shell and from a similar site in the residential area.

E. sylvestris

Only taken once and then from a rolled leaf in the cocoa plantation.

E. quinquevittatus

This species was recorded on a few occasions from banana leaf axils in the residential areas. Both Lumsden (1955) and Aders (1917) record it from empty snail shells and the author has found this to be the more typical breeding site in southern Nigeria.

Culex nebulosus

Larvae were only found in the cocoa plantation where they were taken from rolled leaves and the flower heads of *Heliconia*. They were also taken from pineapple leaf axils but on no occasion were they found more than once in any of these sites.

C. ingrami

In this study the larvae were found widely distributed but without any great abundance in banana leaf axils, rolled leaves and ground pools.

C. annulioris

Hancock (1935) recorded what was probably *C. annulioris* breeding in a *Micanthidium* swamp on the northern shores of Lake Victoria and in the present survey one specimen was taken from a ground pool on the edge of the reservoir.

C. perfidiosus

This species was recorded breeding in small numbers in a muddy pool in an experimental rice field.

C. rima

Recorded twice outside the main cocoa growing area and on each occasion in a crab hole. Dalziel (1920) recorded the species breeding in such a site in southern Nigeria.

Aedes simpsoni

During the course of yellow fever research in Africa attention has been focussed on this species and in East Africa it replaces *A. aegypti* in the Bwamba area as the vector of yellow fever. Previously the species has been recorded from a wide range of plant axil sites. The breeding behaviour has been studied by Gibbins (1942). At Tafo it was found breeding in the residential areas where it was the commonest culicine species; it was most abundant in banana leaf axils and less so in pineapple leaf axils. In the cocoa plantation it was recorded twice in the *Heliconia* flower heads.

A. apicoargenteus

Larvae of *apicoargenteus* were not found in any great abundance ; in the cocoa plantation they were taken once from a tree hole, and alongside the reservoir from a rock pool and a few cocoa husks.

A. aegypti

According to all accounts this species is to be found in a wide variety of breeding sites both natural and domestic, but during the Tafo survey it was notably absent. Only on one occasion were larvae found and then in a rock pool on a large outcrop in the centre of the cocoa plantation.

Harpagomyia taeniarostris

The larvae of this species were not abundant but were taken on several occasions in the cocoa plantation, three times in pineapple axils and four in *Xanthosoma* axils.

Uranotaenia ornata

U. ornata was the most abundant culicine species to be found breeding along the edge of the reservoir. Philip (1931), quoting Ingram and de Meillon (1927), reported the larvae of this species in a shady pool in an area under investigation in Zululand and also in rock pools in the Transvaal. At Tafo the typical breeding sites were the leaf axils of pineapples and to a lesser extent those of bananas. It was also found in smaller numbers in pineapple axils in the residential areas.

U. fusca

Philip (1931) recorded this species from rock pools in the Gold Coast and during the present survey it was the most common species in such breeding sites.

U. annulata

Macfie and Ingram (1916) recorded this species from " excavations made by searchers after crabs along the margin of a stream ", and Dalziel (1920) recorded it from a crab hole and tree hole in the Lagos area. Whilst not abundant at Tafo, *annulata* was recorded from crab holes near to the reservoir and once from a rock pool.

U. candidipes

Philip (1931), quoting Ingram and De Meillon (1927), recorded crab holes as the breeding site of this species ; it was taken from such sites in the Tafo survey.

CONCLUSIONS

It would seem from this survey that the mosquito species had well defined areas of breeding and within these areas preferences for particular breeding site types. For instance, *E. chrysogaster* bred most abundantly in the cocoa plantation and showed a preference for decaying cocoa husks, *E. oedipodius* also in the cocoa was almost entirely restricted to rolled leaves. *U. ornata* was to be found most abundantly alongside the reservoir, breeding in pineapple leaf axils, whilst *A. simpsoni* was largely restricted to the residential areas and bred most abundantly in banana leaf axils. *U. fusca* was only found in rock pools alongside the reservoir. Furthermore, each of the major areas seemed to have a dominant culicine species, *E. chrysogaster*, *U. ornata* and *A. simpsoni* playing these roles in the cocoa plantation, reservoir and residential areas respectively. It is interesting to note that within the cocoa plantation 14 culicine species were recorded, whilst only eight different species were found in both the reservoir and residential areas.

SUMMARY

During an investigation into the breeding places of biting flies at Tafo in southern Ghana during the rainy season 1956, information was collected on the breeding sites of 19 culicine species.

The ecological distribution of each is described.

It was concluded that each species had a restricted area of breeding and within these areas a marked breeding site preference.

The greatest variety of species was found in the cocoa plantation.

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A TECHNIQUE FOR THE EXAMINATION OF THE FEEDING MECHANISM IN PHYTOPHAGOUS HETEROPTERA

By M. G. Emsley

(*Imperial College of Tropical Agriculture, St. Augustine, Trinidad*)

In the course of studying the feeding mechanism of Hemiptera, difficulty was encountered in obtaining plant material with the stylets of the feeding insects *in situ.* Various methods using hot wax, hot and cold fixatives, and anaesthetics were tried but without much success.

The present method is similar to that of Ledbetter and Flemion (1954), in that the insects are killed with a high voltage electric current during the act of feeding. But it differs in that the electrocution is carried out without conditioning or disturbing the insect, and can even be used in the field.

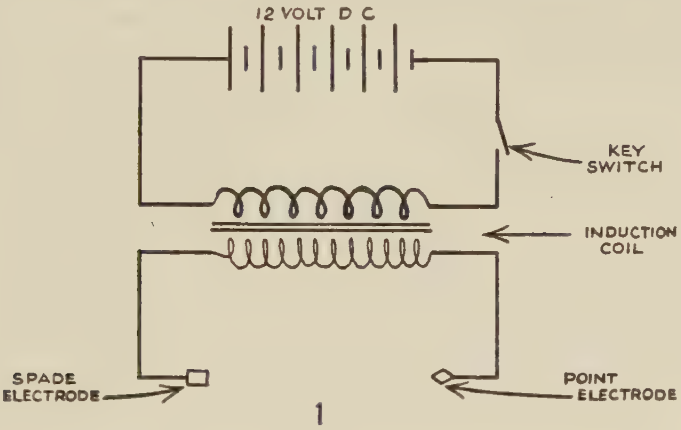

Fig. 1.—For explanation see text.

The source of current used was a secondary cell accumulator of 12-volt output and an induction coil from a motor-car. This combination produced a spark capable of bridging a gap of between one-half and three-quarters of an inch. The actual voltage developed was not measured.

Figure 1 shows the circuit diagram and figures 2 and 3 the actual shape of the electrodes.

If suitable components are used the dimensions of the whole outfit need not exceed 7 inches by 6 inches by 10 inches, and the weight about 10 pounds.

To operate, the flat copper electrode is pushed into the soil at the roots of the plant upon which the insect is feeding and, with the current switched on, the rod electrode is pointed at the insect and slowly brought nearer. At about half an inch distance, more or less, depending on the conductivity of the soil and plant, a spark will jump the gap and be conducted through the insect and plant to earth.

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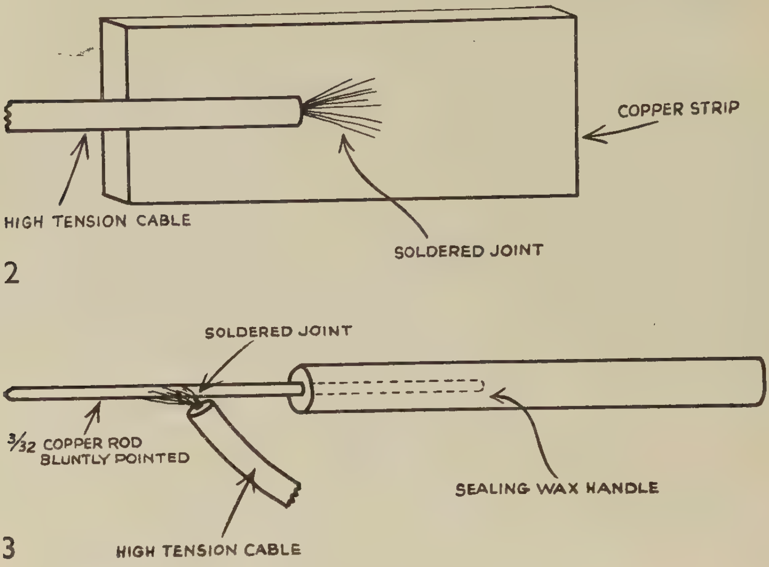
To be more economical on the life of the battery, the current may be switched off until the insect and electrode are in the required position, when switching on will produce the spark instantaneously.



Figs. 2–3.—For explanation see text.

The insect collapses immediately it receives the shock and in all the examples studied there was no evidence that the stylets had been withdrawn at all. Nor was any burning visible in the material when later sectioned. It would appear that the legs are the main conductors of the current.

Most of the work was performed upon plants grown in moist soil in seed boxes. In the field, under somewhat drier conditions, it was necessary on occasions to water the plants before the experiment in order to increase the conductivity.

After electrocution the stylets should be severed at the base of the rostrum and the plant material cut out and fixed in the normal way before sectioning.

Summary

A method of electrocuting Heteroptera whilst in the act of feeding is described.

Acknowledgments

The author would like to thank Miss M. C. Ledbetter and Miss F. Flemion for persuading him to publish this note.

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BOOK NOTICES

Sugar Beet Pests. By F. G. W. Jones. [Bull. Minist. Agric. Lond. No. 162.] 8vo. London (H.M.S.O.), 1957. Pp. vi, 63, text illust. 6*s*. 6*d*.

This work provides the grower with a comprehensive illustrated guide to the identity of the pests of sugar beet, with advice on their control.

The methods of examining seedling and mature plants for pests are described, with tabulated details of the symptoms of attack at all stages.

Pests of the seedling plants and of the established crop are then dealt with in detail, with notes on the life history, type of injury, incidence of attack, and methods of control for each. In the case of the two major pests of the mature crop, aphids and eelworms, information is also given on forecasting outbreaks, virus symptoms and the virus cycle.

The illustrations, comprising eight coloured, eight half-tone plates and many line drawings greatly add to the value of the work.

Spiders, Scorpions, Centipedes and Mites. By J. L. CLOUDSLEY-THOMPSON. 8vo. London (Pergamon Press), 1958. Pp. xiv, 228, text illust. 50*s*.

The author in his introduction indicates the complexity of factors influencing the ecology and distribution of animals, and one of the main objects of this work is to suggest some of the innumerable problems awaiting elucidation and to provide a guide to sources for the identification of the British species, in particular, of spiders, scorpions, centipedes and mites.

A chapter each is devoted to Woodlice, Millipedes, Centipedes, Scorpions, Solifugae, False-Scorpions, Whip-Scorpions, Harvest-Spiders, Spiders, Mites and Ticks, and other " Myriapods ".

The classification and distribution, behaviour, food and feeding habits, enemies, reproduction and life cycle are given, with a list of relevant literature, for each group. A general bibliography, classificatory index, glossary and index of scientific terms and index of general topics complete the work.

Studies on the comparative ethology of Digger Wasps of the genus Bembix. By HOWARD E. EVANS. Cornell Studies in Entomology. 8vo. Ithaca, N.Y. (Comstock Publishing Assoc.); London (Constable), 1957. Pp. ix, 248, text illust. 37*s*. 6*d*.

The author in his introduction explains that this work is an attempt to describe the innate behaviour patterns of several North American species of *Bembix* as objectively as possible, 13 species being dealt with in detail.

The species are then compared with respect to specific behaviour patterns in an attempt to find homologies, modifications and losses and new acquisitions in behaviour. From these data, used in conjunction with morphological, ecological and geographical data an attempt is made to draw conclusions regarding the evolution of behaviour in the genus *Bembix*.

A list of relevant literature and a general index complete the work.

Collecting, preserving and studying insects. By H. OLDROYD. 8vo. London (Hutchinson), 1958. Pp. 327, text illust. 25*s.*

This volume provides an up-to-date account of the equipment and methods used in building up a collection of insects, written in terms that are clear to the beginner and yet detailed enough to serve as a permanent work of reference.

The work is presented in three main sections, Chapters I–IV comprising the first section on collecting insects. Hints are given on where to look ; catching and trapping ; keeping, breeding and rearing ; and killing and temporarily preserving.

The second section (Chapters V–VII) deals with preserving and examining insects. Preparing and mounting for permanent preservation, examining insects in a collection and photographing them are dealt with in detail.

The third section (Chapters VIII–XII) on studying insects, deals with identification and the recognition and description of new species. The principles of zoological classification and nomenclature and the place of insects in the animal kingdom are defined and explained. A list of th Orders of insects is given, with notes on their distinguishing characters and hints on collecting and preservation for each Order.

A chapter is devoted to identification in which the merits of the various types of key are explained, with notes on constructing and adapting keys, a key to the Orders of insects being given as an example and as a first step towards identification.

The major zoogeographical regions are mapped and described briefly. Details are given of the literature which provides basic bibliographical tools, with notes on more general works recommended for further reading. The final chapter gives instruction on writing and illustrating descriptions of new species with advice on where and how to publish.

The appendices which complete the volume comprise a list of useful formulae and reagents, a glossary of terms used in entomology, a list of references, addresses of suppliers of entomological materials, cabinets and books, and an index to the volume.

There are 15 photographic plates and numerous line drawings showing both equipment and details of insect structure.

OBSERVATIONS ON THE MORPHOLOGY OF THE HEAD AND MOUTHPARTS IN THE THYSANOPTERA

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Introduction

There are many conflicting interpretations of the skeletal structures of the head and mouthparts in the Thysanoptera. I believe that some difficulties in determining the probable homologies of the parts concerned can now be resolved in the light of what is known of the muscular system. The following notes therefore aim at suggesting a few new interpretations and at confirming others which up to now have been inadequately supported. Before doing this, however, it is worth commenting briefly on the value of musculature in deciding the homologies of skeletal structures. Snodgrass (1935, 1947, *etc.*) has demonstrated that the relatively constant positions of muscle origins and insertions provide valuable criteria of homology for skeletal parts, though there are undoubtedly cases where muscles have come to occupy unusual positions. Thus, in the Siphunculata, the loss of the tentorium is accompanied by the displacement of tentorial muscle origins on to the wall of the head capsule (Stojanovich, 1945), while Hinton (1948) and Chiswell (1955) have successfully shown the limitations of some of Snodgrass' criteria in homologising the parts of the frontoclypeal region in the head of larval Lepidoptera and Tipulidae. Nevertheless, there are many instances where a consistent and apparently sound interpretation may be developed from studies of musculature (together with other anatomical landmarks) and until additional criteria are available, or until undue reliance on musculature in this particular case involves one in contradictions, it seems worth applying such considerations to the disputed homologies of the Thysanopteran head and mouthparts.

The original findings reported here are based on *Limothrips cerealium* Haliday, the musculature of which was studied in serial sections cut at 6μ after double-embedding by a modification of the technique of Péterfi (1921) and stained with Ehrlich's haematoxylin and eosin. It is hoped to publish elsewhere a full account of the musculature of this species ; only those muscles relevant to a discussion of the following skeletal structures are discussed here :

1. Labrum, clypeus and frons.
2. Tentorium.
3. Maxilla.
4. Labium.

The arguments which follow refer only to the adult, but unless otherwise mentioned the conclusions apply equally well to the second larval instar, which has also been investigated in *Limothrips* by similar techniques.

LABRUM, CLYPEUS AND FRONS

In facial (*i.e.* topographically ventral) view, the Thysanopteran head shows three main regions. There is (*a*) an apical region in the form of an asymmetrical truncate triangle which forms most of the anterior surface of the oral cone ; basal to this is (*b*) a broad, asymmetrically transverse, semimembranous strip which separates the front of the oral cone from (*c*) the main part of the facial surface of the head, extending forwards to the apex. These three regions have been variously interpreted. Thus, considering only some more recent work, Reyne (1927) and Doeksen (1941) refer to them respectively as labrum, clypeus and frons, while Snodgrass (1935) re-interpreted data due to Peterson (1915) and Reyne (1927) to show that (*a*) was the labrum and (*c*) the clypeus, leaving (*b*) without discussion. Again, Pesson (1951) regards the first two structures as containing parts of a subdivided clypeus and the third as the frontoclypeal region. The older interpretations, which will only be discussed incidentally here, show little understanding of modern morphological concepts, but the later work takes some account of musculature and some of the differences of opinion are due to conflicting descriptions and interpretations of the cephalic muscles. The musculature of *Limothrips cerealium* conforms closely to that described by Reyne (1927) for several other species and these data form the basis of the following discussion.

The distal triangular sclerite of the oral cone must certainly be regarded as the labrum, as Reyne (1927), Börner (1929), Snodgrass (1935) and some older workers (*e.g.*, Burmeister, 1936) suggest. This is supported by the fact that both Reyne and I find that it has two sets of associated muscles which correspond to the labral compressors (fig. 1, *lab.comp.*) and the anterior labrals (fig. 1, *lab.a.*) of more generalised insects (Snodgrass, 1935). Reyne also describes another bifurcate muscle, present only on the left-hand side, which appears to be the posterior labral of Snodgrass (1935) but which is apparently absent in *Limothrips*. Other accounts of this region all contain contradictions. Thus, although Melis (1935) identified the sclerite as the labrum in *Liothrips oleae*, his description of the musculature is such that, if correct, it differs in several respects from that of the normal insect labrum and from the descriptions by Peterson (1915), Reyne (1927) and myself for other species of Thysanoptera. Peterson (1915) and Muir and Kershaw (1911) interpreted the triangular sclerite as the clypeus, apparently because they overlooked the anterior labral muscles, whose insertions normally define the basal limit of the labrum. Such a view is certainly disproved by those species in which the anterior labrals are present and is also at variance with the position of the anterior tentorial pits, which Peterson interpreted wrongly (*see* Reyne, 1927). Pesson's (1951) interpretation seems to follow Peterson and is similarly incorrect.

Reyne's (1927) interpretation of the semimembranous region proximal to the labrum as the whole of the clypeus is based on three arguments : (*a*) its lower border is defined by the insertion of the anterior labral muscles ; (*b*) the greater part of the facial aspect of the head is the frons because it bears the origins of the " pharyngeal muscles " and (*c*) the lower boundary of the frons is defined by the site of attachment of the mandible. The first of these points shows only that the region concerned could be the anterior part of the clypeus or an enlarged labroclypeal suture; the second involves a misinterpretation of the dilator muscles of the sucking-pump (as shown below), while the third does not enable one to define the lower boundary of the frons since the primitive mandibular articulation is with the clypeus (Snodgrass, 1950). Furthermore, the position of the anterior tentorial pits does not conform with Reyne's interpretation since they are located on what he calls the frons. His suggestion that these tentorial structures are dorsal arms conflicts with his own discovery (which I have confirmed) that they are invaginations of the wall of the head and that the so-called left anterior tentorial pit of Peterson (1915) does not exist. It is also probable from what is said below that the clypeus extends over much of the more anterior facial aspect of the head. It is therefore clear that this semimembranous area cannot represent the whole of the clypeus. It could conceivably be equivalent to the anteclypeus of more generalised insects or to an enlarged labroclypeal suture but there are no available criteria for deciding which of these views is correct. Börner's (1904) use of the non-committal term "clypeolus" for this morphologically debatable region is probably acceptable.

The muscles which arise from the main facial region of the head, and which are therefore relevant to an interpretation of this area are: (*a*) the anterior labrals (fig. 1, *lab.a.*) and (*b*) the dilator muscles of the sucking-pump (fig. 1, *cib.d.a.*, *cib.m.v.a.*, and *cib.m.v.p.*). The anterior labrals arise typically on the frons and seem therefore to disprove the contention of Börner (1929) and Snodgrass (1935) that the facial region is clypeal in nature, while supporting Reyne and Pesson in their view that it is wholly or partly frontal. However, displacement of the origins of the anterior labrals on to the clypeus is thought to occur in the Diptera (Snodgrass, 1935), so the evidence provided by these muscles is somewhat ambiguous. The sucking-pump is regarded by Reyne (1927), without evidence, as pharyngeal and he is at least consistent in thinking that the origin of its dilators from the facial aspect of the head prove the latter to be the frons. Snodgrass (1935), on the other hand, asserts—also without evidence—that the pump is cibarial and therefore treats the region on which its dilators arise as the clypeus. Obviously the position of the frontal ganglion of the stomatogastric nervous system needs to be taken into account here, as this typically lies between the insertions of the cibarial and pharyngeal dilator muscles (Snodgrass, 1947). Reyne, who states that the frontal ganglion is single in some genera and double in others (including all the Terebrantia he studied) does not indicate its relation to the insertions of the sucking-pump muscles. In *Limothrips*, however, all these muscles converge on to a complex apodeme which lies between the morphologically anterior surfaces of the paired frontal ganglia (fig. 1). There are certainly no sucking-pump dilators inserted posterior to the frontal ganglia and this seems to prove that the pump is cibarial and the main facial region of the head is clypeal. Moreover, since the origins of the more anterior cibarial dilator fibres extend on to the anterior dorsal side of the head between the antennae, there is apparently no frontal element involved in the facial region. So far as one can tell from their figures, similar conditions occur in the species studied by Peterson (1915) and Melis (1935), though the situation is complicated a little by the fact that they and Reyne (1927) describe two sets of dilator insertions on the sucking-pump. The more posterior of these muscles crosses the others and inserts further back from the apex of the head. This more posterior insertion has led Pesson (1951) to suppose that the muscle concerned is a true pharyngeal dilator, that the part of the facial region on which it arises is the frons and that the clypeus and frons therefore " interpenetrate " each other on the face (which he calls the frontoclypeus). The crux of the matter is whether the more posterior of these dilators arises posterior to the frontal ganglia. There is no evidence that this is the case and Pesson's interpretation seems an unnecessary complication in the present state of our knowledge. The main facial region of the head is therefore regarded, on my interpretation of the musculature, as the clypeus, including all of the postclypeus and perhaps some or all of the anteclypeus. This view is quite consistent with the position of the anterior tentorial pits, since the frontoclypeal boundary is commonly curved forwards between them to the apex of the head (*e.g.*, Psocoptera, some Homoptera).

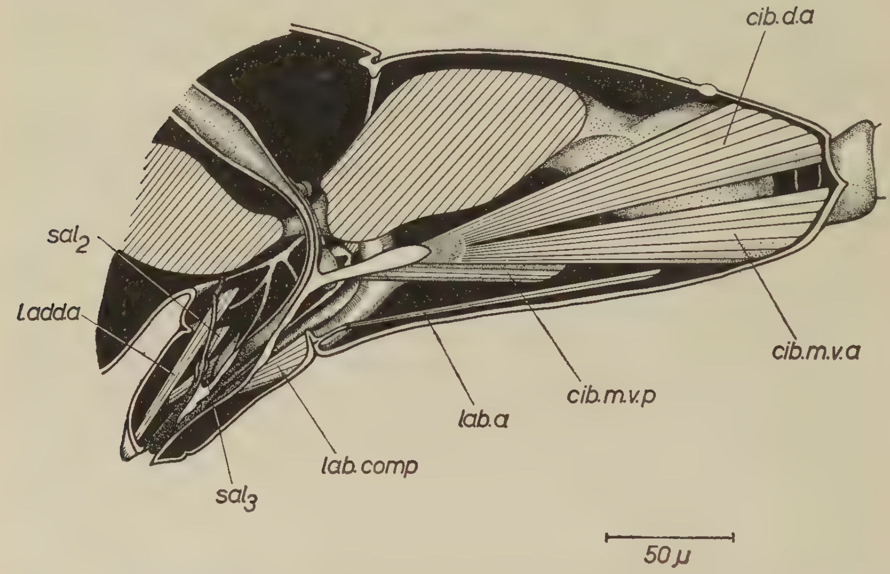

FIG. 1.—Cephalic musculature of adult female *Limothrips cerealium*, left-hand side, viewed from sagittal plane. Reconstructed from serial sections. *cib.d.a.*, dorsal anterior dilator of cibarium ; *cib.m.v.a.*, median ventral anterior dilator of cibarium ; *cib.m.v.p.*, median ventral posterior dilator of cibarium ; *lab.a.*, anterior labral ; *lab.comp.*, labral compressor ; *l.add.a.*, anterior labial adductor ; *sal$_2$*, *sal$_3$*, second and third salivary muscles of labium.

If the above account is correct, the frons must lie on the dorsal side of the Thysanopteran head. The absence of true pharyngeal dilator muscles makes it impossible to delimit the region more precisely, but the origin of the mandibular retractor muscle and the maxillary retractors (which arise from the vertex of more generalised insects) fairly far forwards on the dorsal surface of the head suggests that the frons is restricted to a small region in the neighbourhood of the dorsal ocelli.

THE TENTORIUM

Börner (1904) pointed out the great reduction of the Thysanopteran tentorium, but its detailed interpretation has led to much confusion. Certain structures described in *Heliothrips* by Peterson (1915) and others found in *Melanthrips* by Melis (1933) do not seem to occur in *Limothrips*, nor were they noted by Reyne (1927) in his study of several genera. Reyne did, however, describe two paired cephalic apodemes which are easily identified in serial sections of *Limothrips*. The anterior ones arise from the facial region of the head below the eyes and from their position and the attachment to them of the extrinsic antennal muscles they are evidently tentorial arms. Börner (1904) referred to them as " dorsolateral arms "—which are not recognised by modern morphologists—and Reyne held, from the fact that they provide attachments for the antennal muscles, that they were probably the dorsal arms. This can hardly be true, however, for they are clearly invaginations of the wall of the head capsule (as Reyne himself pointed out) and it seems therefore that they must be composed, at least in part, of the anterior arms. Whether they also incorporate the dorsal arms—to which the extrinsic antennal muscles are normally attached —or whether these muscles have shifted on to the anterior arms through loss of the dorsal outgrowths, is not clear, but the absence of any recognisable dorsal arms makes the latter assumption more probable. Pesson (1951) and Jones (1954) regarded them as anterior arms, though without discussion of the facts involved. Doeksen (1941) appears to have confused various skeletal inflections in the labroclypeal and occipital regions with parts of the tentorium.

The posterior pair of cephalic apodemes arises near the junction of the posterior surface of the oral cone with the prosternum where the subgenal region of the head adjoins the membranous cervix. They were identified as the posterior tentorial arms by Reyne (1927) on the sole grounds that, as in such Orthoptera as *Acheta* (Voss, 1905)—and also *Dissosteira* (Snodgrass, 1928)—they provided an anterior attachment for certain longitudinal ventral muscles of the prothorax. In *Limothrips*, however, my sections show clearly that these muscles are attached on the fold of membrane a short distance behind the apodemes and a similar insertion also holds for the premental adductors and one pair of protergal muscles, both of which Reyne says arise from the apodemes. On the other hand, I agree with Reyne that there is another pair of protergals running from the apodeme and that the hypopharyngeal retractors go from the apodemes to the fulturae of the hypopharynx. Maki (1938), who deals only with one of the protergals and the ventral longitudinals, says that they arise on the " cervical sclerites " which he does not discuss further and which are not otherwise known to occur in the Thysanoptera. It seems likely that the cervical sclerites of Maki are the posterior apodemes of Reyne and myself. Now if one considers in more generalised insects (Snodgrass, 1928; 1935) the attachments of the muscles which are, with little doubt, homologous with the five mentioned above, one finds that three of them (longitudinal ventrals, premental adductors and hypopharyngeal retractors) typically have a tentorial origin,while the other two (first and second protergals) are inserted on the first and second cervical sclerites respectively. To the Thysanopteran apodeme proper, therefore, there are attached two muscles of which one is typically tentorial and the other typically cervical, while to the fold immediately behind the origin of the apodeme are attached three muscles of which two are tentorial and one cervical. The first cervical sclerite articulates primitively with the head very close to the origin of the posterior tentorial arms, and it therefore seems probable that the loss or modification of the cervical sclerites and the reduction of the tentorium in the

Thysanoptera are accompanied by the attachment of their muscles on or immediately behind an apodeme which cannot with certainty be homologised with either cuticular structure.

THE MAXILLA

The maxilla of the Thysanoptera has been the subject of much controversy. Some earlier workers like Uzel (1895), Jordan (1888) and Börner (1904; 1929) regarded the paired stylets as mandibular structures. Garman (1890), however, had already recognised that in the Terebrantian adult each is connected to a maxillary plate by a lever and Buffa (1898), Hinds (1902) and Peterson (1915) followed him in regarding them as maxillary in origin. This identification was further confirmed when Reyne (1927) showed that the embryonic maxillary lobe divides after blastokinesis into a basal part, from which the stylet matrix and stylet arise, and an apical portion which forms the maxillary plate (actually a hollow, lobe-like, pyramidal structure whose inner walls are largely membranous where they are pressed against the labium, hypopharynx and labrum). Basing his further analysis on an interpretation of adult musculature which made use of incomplete data on the generalised maxillary muscles, Reyne then concluded rather tentatively that the basal constricted part of the maxillary plate included the cardo and part of the stipes, while the remainder of the plate was stipital. The galea and lacinia he regarded as probably fused indistinguishably with the apical part of the stipes, while the stylet—and apparently also the lever—he was forced to treat as a secondary process of the cardo or cardo-stipital region. At the same time he, like many earlier authors, was struck by the similarities between the stylet-bearing maxillae of the Psocoptera, Hemiptera and Thysanoptera, though he was not able to attempt a detailed comparison as the Psocopteran maxilla was not then properly understood. Weber (1933), Snodgrass (1935) and Pesson (1951) go no further than Reyne, whose embryological work seems at least to have disposed of all theories that the stylets are mandibular, epipharyngeal or hypopharyngeal (Hansen, 1930). Doeksen (1941) regards the stylets as laciniae but does not cite any supporting evidence.

In *Limothrips* there are four muscles associated with each maxilla. These are:

(*a*) The levator of the palp, arising on the inner, lightly sclerotised wall of the maxillary plate and inserting on the base of the palp;

(*b*) an intrinsic palp muscle which is not relevant here;

(*c*) the stylet protractor, arising from the posterior apical wall of the maxillary plate and inserting on the ventral surface of the maxillary lever; and

(*d*) the stylet retractor, arising from the laterodorsal wall of the head behind the eye and inserting on the base of the stylet near its junction with the lever.

If one compares these muscles with those of a generalised Orthopteroid form (Snodgrass, 1935) it becomes possible to suggest a number of homologies for parts of the Thysanopteran maxilla which differ in many respects from those of Reyne and other writers. The levator of the palp arises typically on the posterior wall of the stipes so that the maxillary plate of Thysanoptera is wholly or partly stipital, as Reyne himself considered. The only other muscles arising from the stipes of primitive insects are the stipital adductor and the stipital flexor of the lacinia. The stylet protractor of the Thysanoptera is therefore probably a homologue of one of these, and the choice obviously falls on the stipital flexor of the lacinia since (*a*) the stipital adductor is an extrinsic maxillary muscle, typically connected to the tentorium, whereas the stylet protractor and the stipital flexor of the lacinia are both intrinsic maxillary muscles ; (*b*) if the stylet protractor were the stipital flexor of the lacinia one would expect it to be inserted on a structure (the lacinia) on which the only other inserted muscle, as in primitive forms, is a cranial flexor. The stylet protractor is, in fact, inserted on the maxillary lever in the adult (and on the lever and adjacent stylet base in the nymphs of some species, according to Reyne) and the only other muscle inserted on the lever-stylet complex of Thysanoptera is the stylet retractor, which therefore seems to be homologous with the cranial flexor of the lacinia.

On this argument, therefore, the maxillary stylet and its lever correspond to the lacinia of more primitive forms and such a view is strengthened by the following considerations : (*a*) Badonnel (1934) found that the retractor of the Psocopteran " pic " arises from the head capsule and this is usually regarded as the most important evidence that the pic is a modified lacinia. A parallel case is well known in the Diptera (Imms, 1944) ; (*b*) the view of Reyne (1927) and Melis (1933) that the maxillary stylet and lever are secondary outgrowths of the cardinal or cardo-stipital region, while not inconsistent with the cranial origin of the stylet retractor—which would then be regarded as the homologue of the anterior cardinal rotator of more primitive insects— is difficult to reconcile with the attachments of the stylet protractor. If this is held to arise on the stipes then their theory encounters the objection that no muscle is known to run from cardo to stipes or from one part of the stipes to another in any insect where these parts of the maxilla are properly recognisable. If, on the other hand, as Reyne suggests, the stylet protractor is inserted on a stipital portion of the lever, then its origin must be from a galea and/or lacinia which is indistinguishably fused with the apex of the stipes—a view for which there is no independent evidence at all ; (*c*) the suggestion of Buffa (1898) and Peterson (1915) that the lever is a modified cardo and the stylet a modified galea is, apart from the obvious objection that the galea does not arise from the cardo in any known insect, made untenable by the arguments mentioned in (*b*) and by the fact that in insects where a galea is indubitably recognisable it never has a cranial flexor inserted on it. Silvestri (quoted by Pesson, 1951) suggested, it is true, that the stylet is the lacinia, but he seems to have relied only on its medial position since he regarded the maxillary plate as the galea, an interpretation which cannot be reconciled with the attachments of the stylet protractors or the palp levators.

The musculature provides no evidence on which one can identify a cardo or cardinal region in *Limothrips* ; at the most it would seem that the extreme outer basal part of the maxillary plate could be of cardinal origin. There is no feature of the skeletal and muscular systems of *Limothrips* to contradict the view that the galea has been lost in the Thysanoptera.

The above arguments, therefore, lead to the conclusion that the maxillary plate is largely or entirely homologous with the stipes, only its extreme outer basal region being perhaps the cardo, while the maxillary stylet and its lever represent the lacinia. It would be out of place here to try to show implications of this view for a comparative treatment of the maxilla in the Hemipteroid orders, but there are certainly indications that all except the highly specialised Siphunculata have a very similar pattern of skeleto-muscular structures.

THE LABIUM

The Thysanopteran labium consists essentially of a strongly transverse basal sclerite and a larger, somewhat cordiform, distal one which bears the small palps and reduced ligula. Buffa (1898) referred to these as the basilare

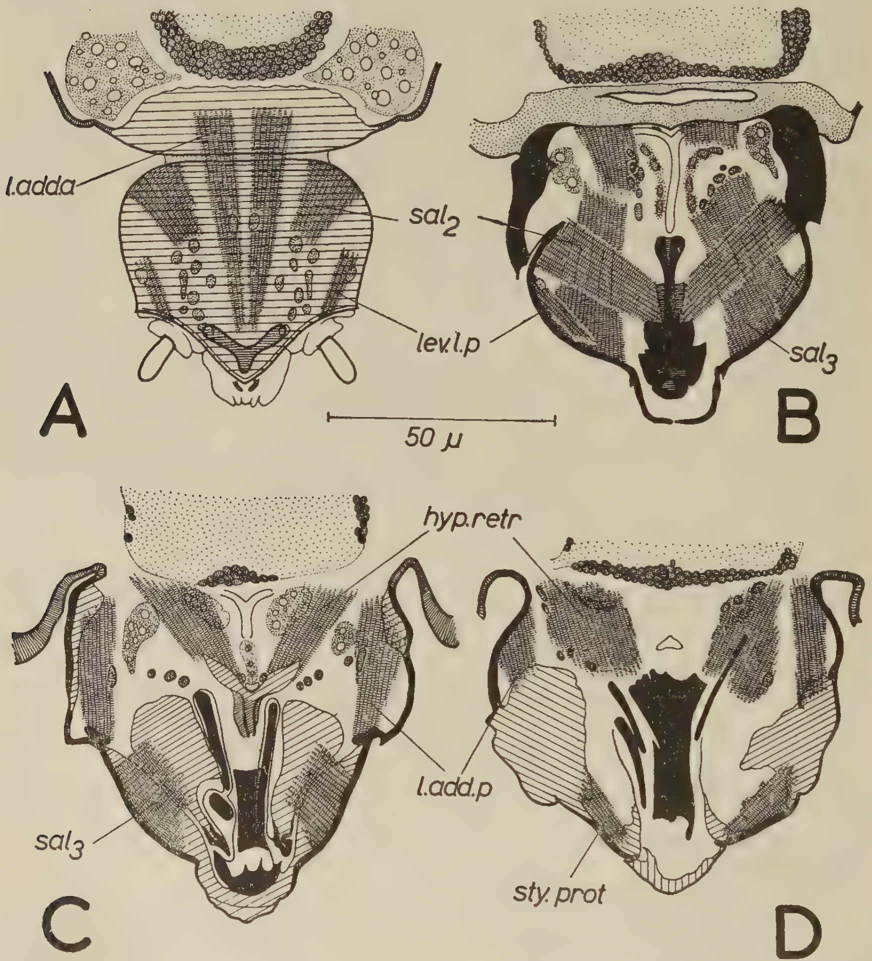

FIG. 2.—Sections through oral cone of adult female *Limothrips cerealium* : A, in long axis of labium ; B, anterior to A, showing hypopharynx ; C, D, anterior to B, showing hypopharyngeal and labial musculature. *hyp. retr.*, retractor of hypopharynx ; *l.add.a.*, anterior labial adductor ; *l.add.p.*, posterior labial adductor ; *lev.l.p.*, levator of labial palp ; *sal*$_2$, *sal*$_3$, second and third salivary muscles of labium ; *sty.prot.*, protractor of maxillary stylet.

and praebasilare respectively, but all subsequent workers (*see* Reyne, 1927; Doeksen, 1941; and Pesson, 1951) denoted them as submentum and mentum until Jones (1954) suggested that a more appropriate nomenclature would be that of postmentum and prementum. From the condition in *Limothrips* illustrated in figure 2 it is now possible to show that Jones's view is the correct one. The attachment of four paired labial muscles—the two salivary muscles (fig. 2, sal_2, sal_3) and the anterior and posterior labial adductors (fig. 2, *l.add.a.*, *l.add.p.*)—on the distal sclerite shows that it is at least partly premental, while the fact that the second salivary muscle and the posterior labial adductor are attached at its basal boundary show that it does not include a mental component (a possibility not eliminated by Jones).

SUMMARY

Previous views on the homologies of some skeletal structures in the head and mouthparts of the Thysanoptera are discussed in the light of their associated muscles in *Limothrips cerealium* Haliday and the following conclusions reached. The clypeus occupies the greater part of the facial aspect of the head and extends on to its dorsal surface for a short distance; the frons is probably confined to a small area near the dorsal ocelli. A pair of anterior cephalic apodemes arising from the face below the eyes are probably the anterior tentorial arms; the musculature associated with a posterior pair of cephalic apodemes suggests similarities with both the posterior tentorial arms and the cervical sclerites. The maxillary plate is largely or entirely homologous with the stipes, while the maxillary stylet and its lever correspond to the lacinia. The two median sclerites of the labium are the prementum and postmentum.

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NOTES ON THE LIFE HISTORY OF *SYMMICTUS FLAVOPILOSUS* BIGOT (DIPTERA: NEMESTRINIDAE) AS A PARASITE OF *SCHISTOCERCA GREGARIA* (FORSKÅL) (ORTHOPTERA: ACRIDIDAE)

By D. J. Greathead

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The first record of a Nemestrinid parasitising Acridids is that of Olliff (1892) who recorded a larva from the Australian Plague Locust *Chortoicetes terminifera* (Walker). Later, Noble (1936) reared adults from similar larvae obtained from the same host in New South Wales. These were *Trichopsidea ostracea* Westwood, which was studied in further detail by Fuller (1938). Crouzel and Salavin (1943) recorded *Neorhynchocephalus sulphureus* Wiedemann and *N. vitripennis* Wiedemann from *Dichroplus arrogans* Stål and *D. elongatus* Stål in the Argentine, and Spencer (1945) noted *N. sackeni* Williston and *T. clausa* Osten-Sacken attacking *Melanoplus mexicanus* Sauss. and *Camnula pellucida* Scud., respectively, in British Columbia. The two last-named species of Nemestrinids have been further studied by York and Prescott (1952) and Prescott (1955), who recorded them from a large number of species of grasshoppers in Montana. *Symmictus costatus* Loew was recorded by Potgieter (1929) from *Locustana pardalina* Walker in South Africa. The only other described species of the genus is *S. flavopilosus* Bigot known from Spain, Algeria and the Caucasus (Sack, 1933). The first record of a Nemestrinid from *Schistocerca gregaria* is that of Shulov (1948) who dissected out a young larva of an undetermined species from an immature male locust in Palestine.

Whilst in the Ogaden province of Ethiopia in December, 1953, the present author found Nemestrinid larvae in hoppers (nymphs) of *Schistocerca gregaria* taken from marching bands, but no adults were obtained. In January, 1954, further larvae were found in Kenya and adults were reared, so that identification of the species became possible. It is assumed that the material from the Ogaden is of the same species as that from Kenya, as the larvae from the two areas are practically identical. In addition, one adult Nemestrinid, of the same species as those reared from *S. gregaria* in Kenya, was taken in the Ogaden immediately before the period when these observations were made. The species proved to be *Symmictus flavopilosus* Bigot, agreeing with the description and type of this species. Some of the specimens have an extension of the chocolate-brown colouring of the veins in the anterior part of the wing on to the surrounding membrane, and this occurs in *S. costatus* Loew according to the description and illustration; the type of *S. costatus* has not been traced. All, however, differ from *S. costatus* in the presence of a veinlet giving rise to an additional cell near the wing tip. It seems possible that when more material is available *flavopilosus* and *costatus* will prove to be a single species.

The following descriptions of the larvae and pupae are based on the material from the Ogaden supplemented by that from Kenya. The larvae were studied from specimens preserved in alcohol and slides were made from specimens macerated in 10 per cent. caustic-potash solution and stained if necessary with benzopurpurin. Specimens macerated and then stained with Pyrogallol and examined in clove oil were found useful for the study of the mouthparts and cuticular folds of the fourth instar. The pupae were studied from exuviae, which retain their shape, and from a single live pupa. More than one specimen was used in the preparation of the drawings of instars.

LARVA

Four larval instars are recorded by Crouzel and Salavin (1943) for *Neorhynchocephalus*, including a minute first instar with long curved bristles on the ventral side. York and Prescott (1952) observed the hatching of such larvae, as well as egg laying, in *Trichopsidea* and *Neorhynchocephalus*. In the present work, three larval instars were found in hopper dissections (Table I); Dyar's Law was applied and confirmed this conclusion. The first instar, which was not found, is probably of short duration and largely occupied in finding the host. The second, third and fourth instars are described below.

TABLE I

Grouping by size	Average length to nearest half-mm.	Average length of " cephalic plate " in units of micrometer eyepiece	Expected length* of " cephalic plate "	Number of larvae measured
1 .	3·0 (range 2·5–3)	8·0 (range 7–9)	.	4
2 .	9·0 (range 6–12)	30·2 (range 27–34)	27·3	35
3 .	14·5 (range 12·5–17)	91·8 (range 77–108)	103	9

* Expected values based on Dyar's Law.

Second Instar (Fig. 1)

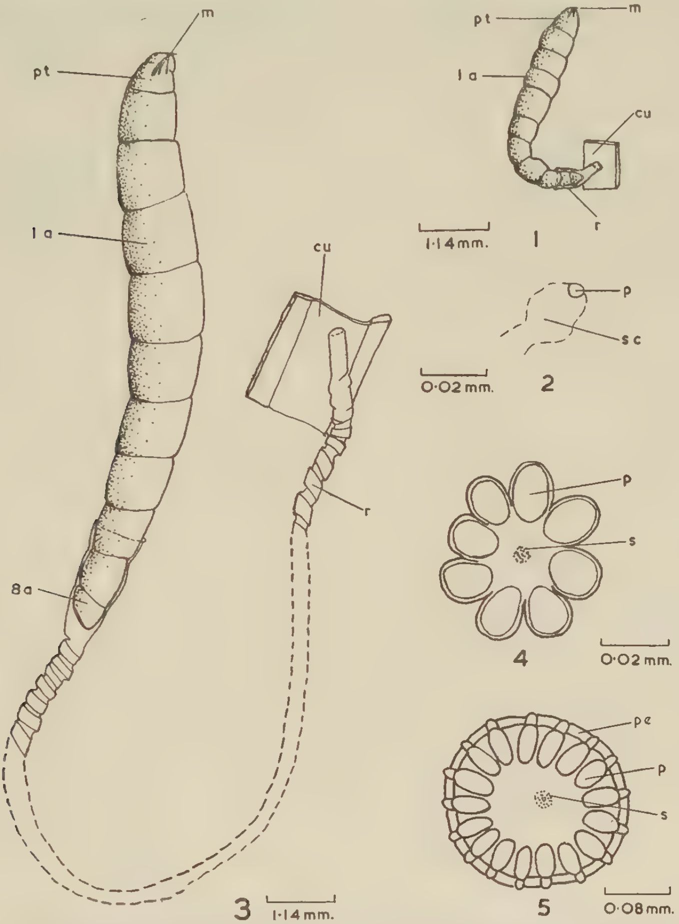
The second-instar larva is 2·5 mm. long, growing to 3 mm., cylindrical, about 0·7 mm. in diameter at the broadest part and tapering bluntly at each end. The cuticle is very thin and transparent. The only pigmented parts are the mouthparts and spiracles. The mouthparts resemble those of the third instar closely, except that they are minute (an oil-immersion objective is required to study them); figures and a description of the mouthparts are given for the third instar, but not the second.

This and the following instars are metapneustic. The spiracle is a simple pore leading into a spiracular chamber; it is borne on the rounded posterior end of the last segment (fig. 2).

Third Instar (Fig. 3)

In this instar the larva varies in length from 6 mm. at the beginning to 12 mm. at the end. In shape it is similar to the second instar. At first it is transparent but later it becomes opaque owing to development of the fat body.

The mouthparts consist of a pair of jaws (termed mouth-hooks by Hennig, 1952) articulating dorsally with an elongate structure (the head plate of Hennig) and ventrally with a pair of tentorial rods (figs. 6 and 7). The mouth-hooks are strongly sclerotised with a strong downward-curved point visible externally. There is a dorsal median articulation, and also a lateral one composed of lateral processes from the mouth-hooks and head plate. A third process projects ventrally from the posterior margin of the base, articulating with the tentorial rods. This arrangement gives a movement in the vertical plane only, as in the mouth-hooks of the Cyclorrhapha. The head plate,

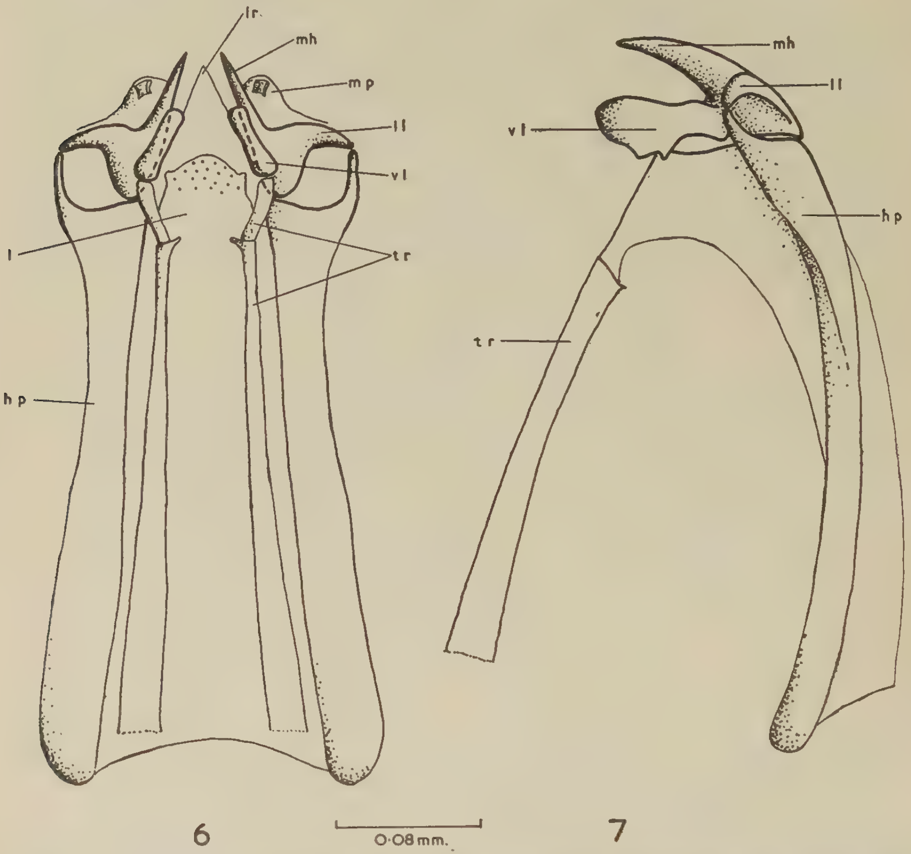


FIGS. 1–5.—Larva of *Symmictus flavopilosus*. (1) Second instar, with respiratory tube attached to integument of host. (2) Spiracle of second instar. (3) Third instar, with respiratory tube attached to integument of host. (4) Spiracle of third instar. (5) Spiracle of fourth instar.

cu, host cuticle; *m*, mouthparts; *p*, spiracular pore; *pe*, peritreme; *pt*, prothorax; *r*, respiratory tube; *s*, scar ("button"); *sc*, spiracular chamber; 1*a*, first abdominal segment; 8*a*, eighth abdominal segment.

which may be a modified epicranium as suggested by Snodgrass (1935), consists of strongly sclerotised lateral rods articulating anteriorly with the mouth-hooks, and united by a thin transparent median sheet. An anterolateral process articulates with the lateral branch of the base of the mouth-hook. Ventral prolongations fuse with the anterior ends of the tentorial rods.

The labrum is a triangular sclerotised plate lying dorsal to the mouth-hooks and forming the dorsal wall of the mouth. There is a ventral fleshy lobe, the hypostomal lobe (Snodgrass, *l.c.*) which forms the ventral margin of the mouth. The antennae and palpi are small thin-walled projections with cylindrical sclerotised endoskeleton. The palpi (presumably vestigial maxillary palps) lie ventrolaterally close to the base of the exposed portion of the mouth-hooks. The antennae are situated behind the palpi and are closer together.



Figs. 6–7.—Larva of *Symmictus flavopilosus*, third-instar mouthparts from dorsal and lateral aspects (palp omitted in fig. 7).
hp, "head plate"; *l*, labium; *lr*, labrum; *ll*, lateral lobe of mouth-hook; *mh*, mouth-hook; *mp*, maxillary palp; *tr*, tentorial rod; *vl*, ventral lobe of mouth-hook.

The spiracles lie close together posterodorsally on the rounded last segment.

They consist of eight circular pores arranged in a ring around a spongy core bearing the scars of the spiracle of the preceding instar (fig. 4).

Fourth Instar (Figs. 8–10)

In the fourth and final stage, the larva measures from 12·5 to 17 mm. in length. At first it is smooth and more or less cylindrical but it soon broadens and becomes flattened ventrally, and it is then about 5 mm. wide at the widest point. The body wall develops a fairly constant series of folds and tubercles which, however, are frequently difficult to see. Eleven segments are visible. The prothoracic segment bears the invaginated head on its ventral side; a raised rim surrounds the mouth-hooks, which are the only cephalic structures projecting externally. The second and third visible segments each have a dorsal row of eight tubercles along the anterior margin, a large lobe on either side bearing a tubercle anteriorly, and a ventral row of ten tubercles along the anterior margin. Segments 4–9 are similar to the second and third but lack the dorsal row of tubercles. Segment 10 has no tubercles; it is enclosed in the end of the respiratory tube when the larva is in the host. The last segment is roughly conical with a dorsal concavity in which the spiracles lie close to the middle line. The rim of this concavity is swollen into a series of tubercles, five of which lie around the posterior margin and six, less well defined, are on the anterior margin; there are four more tubercles on the floor of the cavity inside the margin. The anus is situated ventrally near the posterior end in a slight concavity.

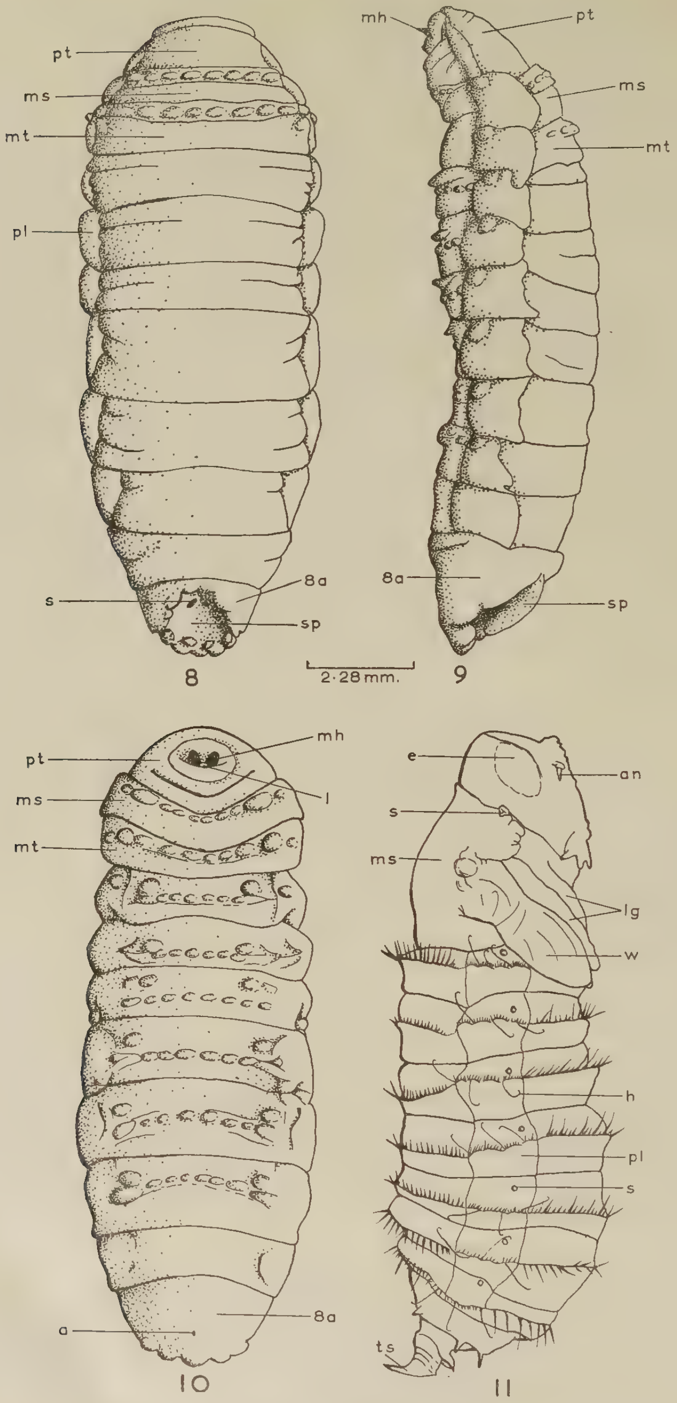
The mouthparts (figs. 12–14) differ markedly from those of the previous instars. The mouth-hooks are broad, flattened and spade-like. The articulation with the head plate is diagonal in the horizontal plane. The ventral lobe is greatly enlarged and produced posteriorly below the tentorial rods. The U-shaped, heavily sclerotised, part of the head plate is more massive but is produced laterally and posteriorly in a thin ill-defined sheet. The labrum is a dorsal triangular lobe and the hypostomal fold is well developed and its surface pitted by large sensillae. The antennal vestige is dorsal to the posterior margin of the mouth-hooks. The maxillary palp is now more conspicuous and clearly two-segmented.

The other structures are the drumstick-like tentorial rods lying below the head plate and articulating anteriorly with the ventral edge of the anterior end of the U-branches of it. The ventral wall of the pharynx is well sclerotised and lies within the space enclosed by the head plate and tentorial rods.

The spiracles are circular, each with a ring of 18–20 oval slits inside a strong peritreme. The walls of the slits are produced at the outer edge into dense, highly sclerotised knobs. The central part of the spiracle is a fibrous mass, with the scar of the preceding instar near but not at the centre of it (fig. 5).

The Respiratory Tube

This structure, which was found associated with all the *Symmictus* larvae in dissections of the hosts, consists of a tube of brown substance resembling cuticle connecting the larva with the body wall of the host (Plate I, fig. 3). The end attached to the host appears as a minute brown scar in the intersegmental



FIGS. 8–11.—For explanation see facing page.

membrane of the host and represents the point of entry of the larva (Prescott, 1955). A marked preference for the prothoracic-mesothoracic membrane was found in the material studied ; no larvae were attached in front of this membrane and very few behind it (Table II). The tube is spirally thickened in a characteristic manner (fig. 3). The end attached to the parasite larva fits over the last two segments and fades into a thin transparent rim. The tube is smooth when first secreted, the thickening developing through collapse of the tube spirally.

TABLE II.—*Position of attachment of respiratory tube of* Symmictus *larvae to hosts* (*Ogaden*, 1953)

Point of attachment	Number of hosts examined
Between prothorax and mesothorax . . .	164
Between mesothorax and metathorax . . .	5
Between metathorax and 1st abdominal segment .	10
Between 1st and 2nd abdominal segments . .	8
Between 2nd and 3rd abdominal segments . .	5
Between 3rd and 4th abdominal segments . .	0
Between 4th and 5th abdominal segments . .	3
Between 5th and 6th abdominal segments . .	1
Between 6th and 7th abdominal segments . .	1
Between 7th and 8th abdominal segments . .	0
Between 8th and 9th abdominal segments . .	1
Total	198

The diameter of the tube is rather less than that of the larva at the time of secretion of each part of it. In the second instar, the length of the tube is little more than that of the last two abdominal segments. During the third instar, it rapidly increases in length so that the larva lies in the abdomen of the host with its head in the same direction as the head of the host. In the fourth instar, the rapid increase in diameter of the larva is coupled with a sharp increase in diameter of the respiratory tube, which, however, grows very little in length in this instar.

The tube is left in its entirety inside the host when the larva emerges from it.

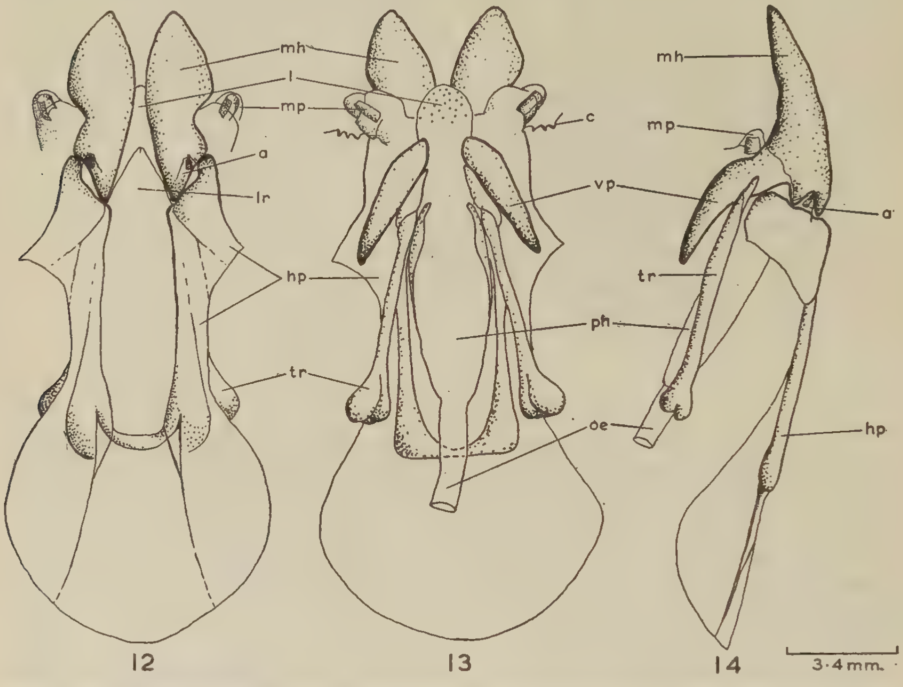
The respiratory tube is similar in all species so far described, though its point of attachment, and therefore the mode and place of entry of the first-stage larva, differ in the species referred to by Prescott (1955). *Symmictus* resembles *Neorhynchocephalus sackeni* in entering the host through the intersegmental membranes, and it resembles *Trichopsidea clausa* in showing a preference for the pro-mesothoracic area, though in this last species entry is by way of the spiracles.

FIGS. 8–11.—Fourth instar (dorsal, lateral, and ventral) and pupa (lateral) of *Symmictus flavopilosus.*

a, anus ; *an*, antenna ; *e*, compound eye ; *h*, hooked bristle ; *l*, labium ; *lg*, leg ; *mh*, mouth-hooks ; *ms*, mesothorax ; *mt*, metathorax ; *pl*, pleuron ; *pt*, prothorax ; *s*, spiracle ; *sp*, spiracular pit ; *ts*, terminal spine ; *w*, wing ; 8*a*, eighth abdominal segment.

Pupa.

The pupa (fig. 11) is about 17 mm. long and 5 mm. in diameter at the broadest part. The shape is striking in that the abdomen is unusually broad, being broader than the head and thorax. The surface of the head and thorax is granulated. The appendages of the adult are not very clearly differentiated. Wings and legs are short, extending over only one segment of the abdomen. The prothoracic spiracles are the only thoracic spiracles visible. They are large, heavily sclerotised and wart-like, and are on the anterior lateral edge of the segment.



Figs. 12–14.—Mouthparts (dorsal, ventral, and lateral) of fourth-instar *Symmictus flavopilosus*.

a, antenna; *c*, cuticle of head; *hp*, "head plate"; *l*, labium; *lr*, labrum; *mh*, mouth-hook; *mp*, maxillary palp; *oe*, oesophagus; *ph*, pharynx; *tr*, tentorial rod; *vp*, ventral process of mouth-hook.

The first seven abdominal segments are similar to one another. Each has very distinct sternal, tergal, and bulging pleural regions. A ring of spines lies around the middle of each of these segments. Dorsally and ventrally the spines are relatively large and strong, but in the pleural region they are small except for three very long hooked bristles on either side of each of these segments. The spines on the first five segments are directed forwards and those on the sixth and seventh backwards. Spiracles are borne on all these segments and are similar to, but smaller than, the prothoracic ones. The terminal segments taper rapidly to a forked structure on the tenth. The eighth segment has three pairs of stout teeth and the ninth has one pair ; the terminal structure has a pair of broad, flattened spines set transversely and pointing dorsally.

Comparison of the drawings and descriptions of Nemestrinid larvae, respiratory tubes and pupae given by Fuller (1938), Crouzel and Salavin (1943) and Prescott (1955) with those in this paper shows that, although the general form of these stages of all the species so far described is similar, the shape of such structures as the mouthparts, especially the mouth-hooks, differs, though this may be partly at least due to the degree of flattening of the preparations and the angle at which they have been drawn. The tubercles of the late fourth instar appear to differ in number and arrangement. The spiracles also differ in the number and shape of the pores. In the pupae, the shape of the cephalic structures was found to be different by Prescott (1955) in *Neorhynchocephalus sackeni* and *Trichopsidea clausa* ; the number and arrangement of abdominal bristles and spines may also be of diagnostic value. In the present state of knowledge it is only possible to suggest that these characters are of taxonomic importance.

LIFE HISTORY

The adult was not observed in the field, except for one male taken in a general collection of Diptera in the Ogaden before locust hoppers had hatched. No information was obtained on the eggs or the mode of entering the host. The youngest stage observed was the small larva described above as second instar. The observations of York and Prescott (1952), Prescott (1955) and Crouzel and Salavin (1943) indicate that the first instar is minute and has long hooked hairs. The second, third and fourth instars were observed in dissections of the third, fourth and fifth instars and fledglings of the locust. The observations made were not sufficiently complete for calculation of the duration of each instar, but the data in Table III indicate that the total length of the period in the host is probably between 9 and 14 days and the preponderance of the third instar indicates that it is the longest and that the increase in size during the fourth instar occurs rapidly. The development of the respiratory tube during the third instar may be the cause of the longer time spent in that instar.

The two North American species lie inside the host with the head forward. *Symmictus* lies in the same position, which may be common to all species parasitising grasshoppers, as the fully grown larva requires a large area of membrane for emergence. The mode of emergence in these three species is similar in that it is generally by rupturing the membranes near the base of the abdomen behind the base of the third leg, and wriggling out (Plate I, fig. 4).

After leaving the host, the larvae are active and quickly burrow into the sand. They have not been found in the field at this stage, but observations made on larvae kept in sand in jars show that they enter a period of inactivity during which contraction occurs and they darken to an orange-yellow colour due to large quantities of yellow oil in the fat body. Larvae from El Rago, Ethiopia, which were kept from December, 1953 to the end of January, 1954 in jars in the field, failed to pupate even though the sand was moistened on several occasions. They were then sent to the Anti-Locust Research Centre in London, where they received the same treatment, but they eventually died, after several more months.

TABLE III.—*Development of* Symmictus *larvae in* Schistocerca *hoppers*

Observations at El Rago, Ogaden, Ethiopia (06° 33′ N., 45° 43′ E.)

Date in Dec., 1953	Percentage of hoppers parasitised	Percentage of hoppers containing larvae in the:			Number of hoppers dissected	Number of hoppers parasitised
		2nd instar	3rd instar	4th instar		
3 . .	23	1	22	0	92	21
4 . .	11	2	9	0	336	38
7 . .	34	10	24	0	98	33
12 . .	17	0	16	1	150	27†
14 . .	23	1	18	4	264	60
17 . .	11	0·5	3	7·5	198	22
Observations at Wajir, Kenya (01° 45′ N., 40° 03′ E.)						
Jan., 1954						
11 . .	0·5	0	0·5	0	200	1
13 . .	0·2	0	0·2	0	500	1
15 . .	2·6	0	2·2	0·4	226	5
18 . .	1·9	0	0	1·9	103	4*
20 . .	1·9	0	1·9	0	106	2

* Including two hoppers from which the parasites had already emerged.

† Including one hopper from which the parasite had already emerged.

The samples were each collected from more than one band of hoppers but within the same locality on the same day.

Five larvae from Wajir behaved in the same way in Africa, but on being brought to London, and placed in a jar of wet sand near a lamp in a constant-temperature room kept at 30° C., they swelled up considerably and two of them pupated and became adult in due course; the pupal period was 10 and 12 days. The other larvae remained in diapause. This irregularity in development shows a close parallel with the Bombyliid, *Systoechus somali* Oldroyd (Hynes, 1947), and presumably favours survival of the species. Hynes found that some of the resting *Systoechus* larvae pupated after being soaked with water, but others did not. Invasions of locust swarms, and the subsequent breeding of them and also the breeding of the resident grasshopper populations, are associated with rainfall. A proportion of the larvae of *Symmictus* and *Systoechus* are therefore likely to be induced, by moisture in the soil, to pupate and to become adult at times when their hosts are available.

Though not completely known, the life history of *Symmictus flavopilosus* is probably similar to that of *S. costatus* as observed by Potgieter (1929) and those of *Neorhynchocephalus sackeni* and *Trichopsidea clausa* described by York and Prescott (1952) and Prescott (1955). Adults emerging after rains probably soon proceed to lay a large number of small eggs in cracks in bark and soil. Minute larvae hatch and blow about. If these encounter a suitable Acridid they enter through an intersegmental membrane. The range of hosts is probably wide and certainly includes *Schistocerca gregaria*, *Aiolopus savignyi* (Krauss) and *Sauracris* sp. Moulting probably occurs soon after the commencement of the formation of the respiratory tube. Three instars then follow over a period of about two weeks, at the end of which time the host is reduced to a starved condition. Emergence follows and the host dies. There is then a long period, possibly up to several years, of resting in the soil, until rain induces pupation and the subsequent emergence of the adults in about two weeks.

Other Hosts

During the period of the observations at El Rago, various grasshoppers were collected and dissected to ascertain if parasites were present in them as well as in locusts. Of 63 *Aiolopus savignyi* (Krauss), one was parasitised by a Nemestrinid, but of four *Oedaleus senegalensis* Krauss and four *Chrotogonus* sp., all were healthy. Whilst collecting grasshoppers at Bio Fogo, between Zeila and Berbera in the Somaliland Protectorate, Mr. G. B. Popov found that most of the specimens of a species of *Sauracris* were parasitised by a Nemestrinid. One adult reared from these proved to be of the same species of *Symmictus* as those from locusts in Kenya. This is of interest as *Sauracris* spp. hide under the bark of dead trees and only emerge for feeding, and York and Prescott (1952) and Spencer (1931, 1932) found *Neorhynchocephalus* and *Trichopsidea* ovipositing in holes and cracks in posts. Though the habits and habitat of the species of *Sauracris* are unusual for Acridids, they would form ideal hosts for *Symmictus* if its oviposition habits are the same as those of the two North American genera.

There is an earlier record, almost certainly of this species, from the Sudan. In the collection of the British Museum there are a headless adult and two larvae, the former labelled : " Um Darag, Sudan, R. C. M. Darling, bred from larva in body cavity of living adult *Schistocerca gregaria* Forsk. 18.viii.32 ; pupal stage 91 days ". The length of the pupal period given is strange, but it probably refers to the whole period from removal of the larva from the host until the emergence of the adult.

Dissections of samples of nymphs of *Schistocerca* and other Acridids collected in Eritrea in February and March, 1954, December, 1955, January, February and November, 1956, and January and February, 1957, as well as samples from the Hadhramaut in June, 1954, all failed to yield Nemestrinid larvae. Nor have any such larvae been found by the writer in extensive surveys of *Schistocerca* egg-fields carried out in these areas, though other workers (*e.g.* Potgieter, 1929) have found the resting larvae in the soil whilst searching for Acridid eggs.

VALUE AS A PARASITE OF THE DESERT LOCUST

Only one parasite larva was found per host in all except three out of 201 parasitised locusts collected at El Rago. The three exceptions contained two each, and all three occurred in one sample of 98 hoppers taken on 7th December. In two cases there were two third-instar larvae, and in the third case there was one second-instar and one very young third. It seems likely that two larvae cannot survive in the same host for long, since two fully fed larvae would be unable to exist together. A fourth-instar hopper is distended by one. No remains of dead larvae were found in any of the hoppers dissected, however, and it is possible that hoppers with two parasite larvae do not survive long. Prescott (1955) also records that there is normally only one Nemestrinid larva per host, except when very young larvae are present ; he considers that physical injury causes the death of all larvae but one.

During the development of the parasite, the host is normal in appearance and activity, but the fourth-instar larva fills the body cavity of a fourth-instar hopper, which then appears distended and has chalky pinkish-white markings instead of the usual yellow ones. Internally, little damage seems to be done until the parasite is nearly fully fed, but at the end of the period of feeding the parasite destroys the fat body and its bulk appears to interfere with feeding as the gut of every hopper dissected at this stage was conspicuously empty as compared with those of healthy members of the same hopper band.

It seems that few hoppers survive the emergence of a *Symmictus* larva. Only one living hopper with evidence of having been parasitised (*i.e.* with a respiratory tube) was found amongst the 1138 hoppers dissected at El Rago, and two were found at Wajir amongst 1135 hoppers dissected. Potgieter (1929) reports that *S. costatus* is not lethal to the adult host. Prescott considers that the life of the host is shortened and the reproductive potential greatly reduced, the eggs being largely destroyed in the later stages of parasitisation. However, Potgieter states that oviposition is not completely prevented.

Two observations indicate the effect of the presence of a larva of *Symmictus flavopilosus* on the development of the host. In the first, it was noted that many fourth-instar stragglers of a band of fifth-instar hoppers were in the distended, discoloured condition described above. Some were caught and torn open, and many contained a fourth-instar *Symmictus* larva. Thirty-two were dissected carefully; only three were healthy, five had second- and third-instar parasites and 24 had fourth-instar parasites. A large sample of hoppers collected by net over the whole band showed a proportion of 827 fifth-instar hoppers to three fourth-instar. The results are summarised in Table IV; 104 fifth-instar hoppers were taken at random and dissected, and only one contained a *Symmictus* larva, almost fully grown.

The second example of the effect on development is taken from a fledgling band (Table IV). The proportion of young fifth-instar hoppers parasitised is significantly greater than that of older ones and fledglings, and this may be due to retardation of development, though it may also be due to mixing of two bands of different ages.

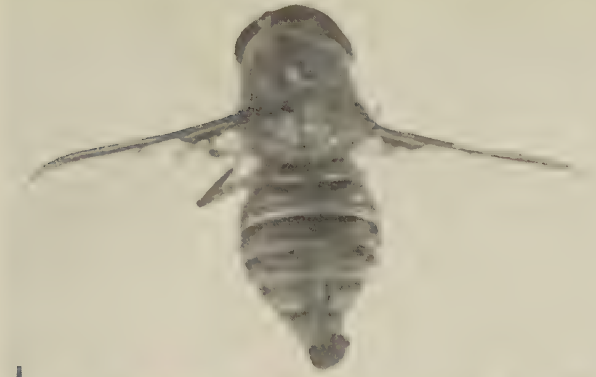
TABLE IV.—*Effect of* Symmictus *larvae on hoppers of* Schistocerca gregaria *at El Rago, Ethiopia*

Date	Instar of host	Number dissected	Number healthy	Instar of parasite			Total parasitised
				2nd	3rd	4th	
14.xii.53	4th	32	3	3	2	24	29
	5th	104	79	0	24	1	25
17.xii.53	Young 5th	42	24	0	3	15	18
	Old 5th	92	88	1	2	1	4
	Fledgling adult	53	52	0	1	0	1
	Total	187	164	1	6	16	23

The parasitisation of young fifth-instar hoppers in the second example shows a highly significant difference ($P < 0{\cdot}1$ per cent.).

The efficiency of this parasite as a natural enemy of *Schistocerca* is hard to evaluate at present, but as is shown in Table III, up to 34 per cent. of hymphs in bands in the El Rago area in December, 1953 were parasitised and probably killed, whereas at Wajir, Kenya, just over a year later, not more than 4 per

PLATE I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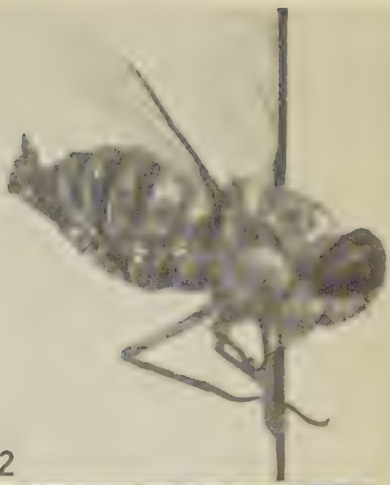
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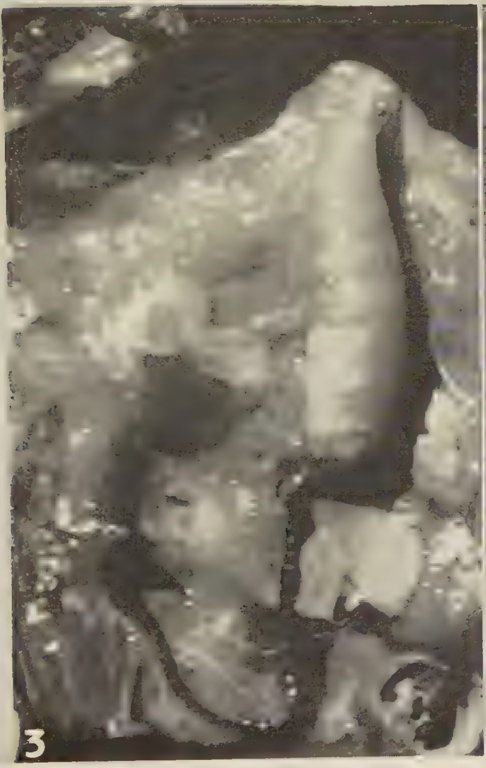
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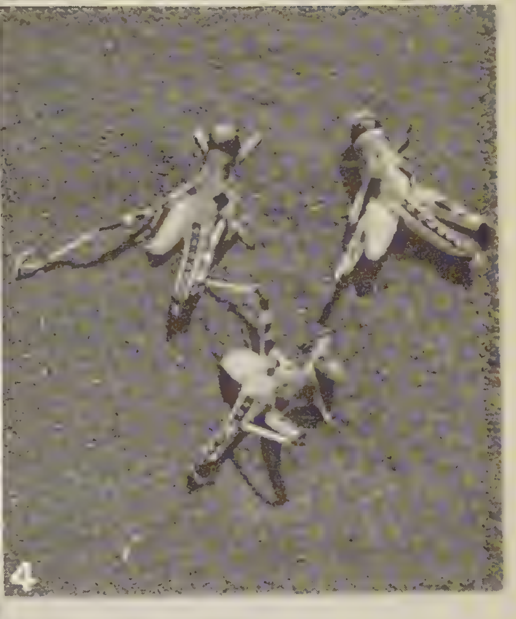
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Symmictus flavopilosus Bigot

FIGS. 1 and 2.—Dorsal and lateral views of adult.
FIG. 3.—Young fourth-instar larva *in situ* in *Schistocerca gregaria* nymph, showing respiratory tube.
FIG. 4.—Fully fed larvae emerging from fourth-instar *Schistocerca gregaria*.

D. J. Greathead.

(Photo. by C. Ashall, Desert Locust Survey.)

cent. were parasitised. Its value seems to vary, but the parasite may at times account for a considerable proportion of locusts in the Somali peninsula.

ACKNOWLEDGMENTS

The author is indebted to Mr. H. Oldroyd of the British Museum (Natural History) for his invaluable help in the identification of the adult material, and to Mr. G. B. Popov, of the Desert Locust Survey, for making available his material and notes on the larvae from *Sauracris.*

The Director of the Desert Locust Survey, Mr. P. R. Stephenson, and many members of his staff have, through their interest and assistance at all stages, made the work possible.

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THE SOURCE OF THE QUEEN SUBSTANCE OF THE HONEY-BEE (*APIS MELLIFERA* L.)

By C. G. Butler and J. Simpson

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Introduction

The queen of a honey-bee colony produces a secretion which is found on all parts of her body surface and is sought by her workers (Butler, 1954, 1956, 1957 ; Butler and Gibbons, 1958). This queen substance controls and normally inhibits queen rearing by the workers. Its origin has remained undiscovered. However, de Groot and Voogd (1954) obtained evidence suggesting that this or an analogous substance, which normally inhibits development of the ovaries of worker honey-bees, is particularly abundant on the queen's head, and Simpson (1956) has suggested that it may be produced in the mandibular glands. This hypothesis has now been tested.

Experimental Technique

A number of well-ventilated Perspex cages, each 60 mm. × 50 mm. × 95 mm. high were used. Each cage was supplied continuously with sucrose-candy and distilled water in separate feeders. One hundred and fifty worker bees were placed in each cage. All the worker bees were taken at random from two normal colonies in which no occupied queen cells were present and which were headed by mated, laying queens. The bees in cages with odd numbers came from one colony, those in cages with even numbers from the other.

A piece of comb, 5 cm. long and 2 cm. wide, consisting entirely of empty worker cells was placed in each cage, and a dead mated queen honey-bee which had been extracted in ethanol in a Soxhlet apparatus for 32 hours was attached to it with a loop of thin wire. For each experiment all the queens concerned were extracted together in the same apparatus.

In some cases (the controls) nothing was added to the extracted bodies of the queens in the cages, in others (the experimental cages) various test substances were added either by smearing (mandibular gland contents, haemolymph, etc.) or by dipping them into the substance concerned (ethanol extracts of queen substance).

All the cages of bees were kept in an incubator at approximately 32° C. After the bees had been confined in their cages for five hours, six worker larvae, each about 12 hours old, were transferred into separate worker cells in the piece of comb in each cage. The cages were immediately returned to the incubator. After a further 16 hours the comb in each cage was examined and the number of emergency queen cells, modified from the cells in which the young worker larvae had been placed, were recorded.

PROC. R. ENT. SOC. LOND. (A) 33. PTS. 7–9. (OCTOBER, 1958).

Experiment I

Cages 1–12.—Controls.

Cages 13–24.—0·10 queen bee equivalent[1] of queen substance in ethanol added to the body of the extracted queen.

Emergency queen cells were built in 11 of the 12 control colonies, but none appeared in any of the 12 experimental colonies. This difference is highly significant ($P < 0{\cdot}001$) and indicates that the bodies of the extracted queens had little ability to inhibit queen cell production by groups of 150 worker bees.

Experiment II

Cages 1–12.—Controls.

Cages 13–24.—Contents of mandibular glands of one queen honey-bee smeared on the body of the extracted queen.

Cages 25–36.—Haemolymph from one mated queen honey-bee smeared on the body of the extracted queen.

Cages 37–48.—0·10 queen bee equivalent of queen substance in ethanol added to the body of the extracted queen.

Emergency queen cells were built as follows :

Cages 1–12.—One or more in each cage.
Cages 13–24.—None in any cage.
Cages 25–36.—One or more in each cage.
Cages 37–48.—None in any cage.

The mandibular gland and queen substance groups are both ($P < 0{\cdot}001$) different with high significance from the control and haemolymph groups.

Experiment III

Cages 1–12.—Controls.

Cages 13–24.—Contents of the mandibular glands of one mated queen honey-bee smeared on the body of the extracted queen. (These were the same extracted queens, with the same mandibular gland contents still on their bodies, as those used in Experiment II.)

Cages 25–36.—Contents of mandibular glands of a worker honey-bee smeared on the body of the extracted queen.

Emergency queen cells were built as follows :

Cages 1–12.—One or more in each cage.
Cages 13–24.—One empty queen cell in one of the cages, none in any other.
Cages 25–36.—One or more in each cage.

Thus the queen mandibular gland group differed with high significance ($P < 0{\cdot}001$) from either of the two others.

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[1] A queen bee equivalent is an arbitrary measure based on the average amount of queen substance per queen that was extracted by soaking the bodies of several hundred mated queens in a given amount of ethanol for about 18 months at room temperature.

Conclusions

It is clear from the results obtained in Experiments I and II that 0·10 queen bee equivalent of queen substance is sufficient to inhibit a small group of queenless worker honey-bees from attempting to rear emergency queens, and also that the mandibular gland contents of a mated queen honey-bee have a similar effect. The haemolymph of a mated queen (Exp. II) and the mandibular gland contents of a worker honey-bee (Exp. III) have little, if any, such effect.

It is noteworthy that the mandibular gland contents of the queens used in Experiment II (3rd June, 1958) persisted sufficiently to inhibit queen cell production when used again in Experiment III (6th June, 1958).

In other experiments neither a mush of the brain of a queen honey-bee, nor a mush of a queen's ovaries, were found to exert an inhibitory effect.

It seems clear, therefore, that queen substance is produced in the mandibular glands of the queen honey-bee. If this is its only source, it would appear that in some way, perhaps during grooming, it must become distributed over the whole body surface of the queen, from whence the workers obtain it.

Summary

Experiments are described which demonstrate that the contents of the mandibular glands of a mated queen honey-bee, but not of a worker bee, are capable of inhibiting queen production by a group of queenless worker honey-bees. No such effect was produced by the haemolymph of a queen or by the crushed brain or ovaries.

It is concluded that the mandibular glands of the queen honey-bee produce queen substance.

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LARVAL MORPHOLOGY OF DIFFERENT GENERA OF AGROMYZIDAE (DIPTERA)

By Pamela Allen

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In a previous paper I have discussed the morphology of Agromyzid larvae and those characters which may be found useful in key construction (1957*a*), and I have also described (1957*b*) larvae of several species of a single genus, *Phytomyza*, in order to gain some knowledge of the degree of intrageneric variation. It is now desirable to examine species of different genera to determine their larval similarities and differences. Species from seven genera are described in this paper. In some it has been possible to describe only features visible in the puparium because few larvae were obtained. Consequently variation in the facial mask of the larva cannot be discussed, but since circumstances force me to end my study of this family I am including these incomplete descriptions for comparison of other characters and in the hope that they will be of value to other workers.

The muscle scar and tubercle band pattern diagrams have been explained in my previous papers. They represent one half of a puparium ; the diagonal stippling symbolises tubercle bands of constant occurrence and the dotted areas represent places where tubercles were found in only some of the material examined. The appearance of a portion of the tubercle band is shown for each species and in all cases has been drawn from the lateral part of the post-fourth abdominal band.

Phytobia (*Dizygomyza*) *iraeos* Goureau (Fig. 1)

Larvae and puparia were collected from mines in the leaves of *Iris pseudacorus* L. at Stromemore, Wester Ross, Scotland, and at Belfast, Northern Ireland.

Pupation takes place within the mine but the spiracles are not elongated to pierce the epidermis. The puparium is very dark, only a little shiny, and fairly smooth, although the dorsal and ventral surfaces may be somewhat flattened and marked by the pressure of the adjacent plant cells. The emergence fracture occurs in the first abdominal segment, but does not usually pass completely round it. Even after treatment with dilute hydrochloric acid to dissolve the calcospherites the puparium remains very hard and brittle, unlike the other species which I have examined.

The muscle scar bands are also unusual, being doubled in the abdominal segments. The scars themselves are transversely elongated and are rather difficult to see until the specimen is stained as, for example, by Basic Fuchsin and Orange G (Hering, 1954).

The tubercles are of medium size, scattered irregularly in the intersegmental bands, which usually occupy 30–40 per cent. of the lateral segment width and form the pattern shown (fig. 1 (5)).

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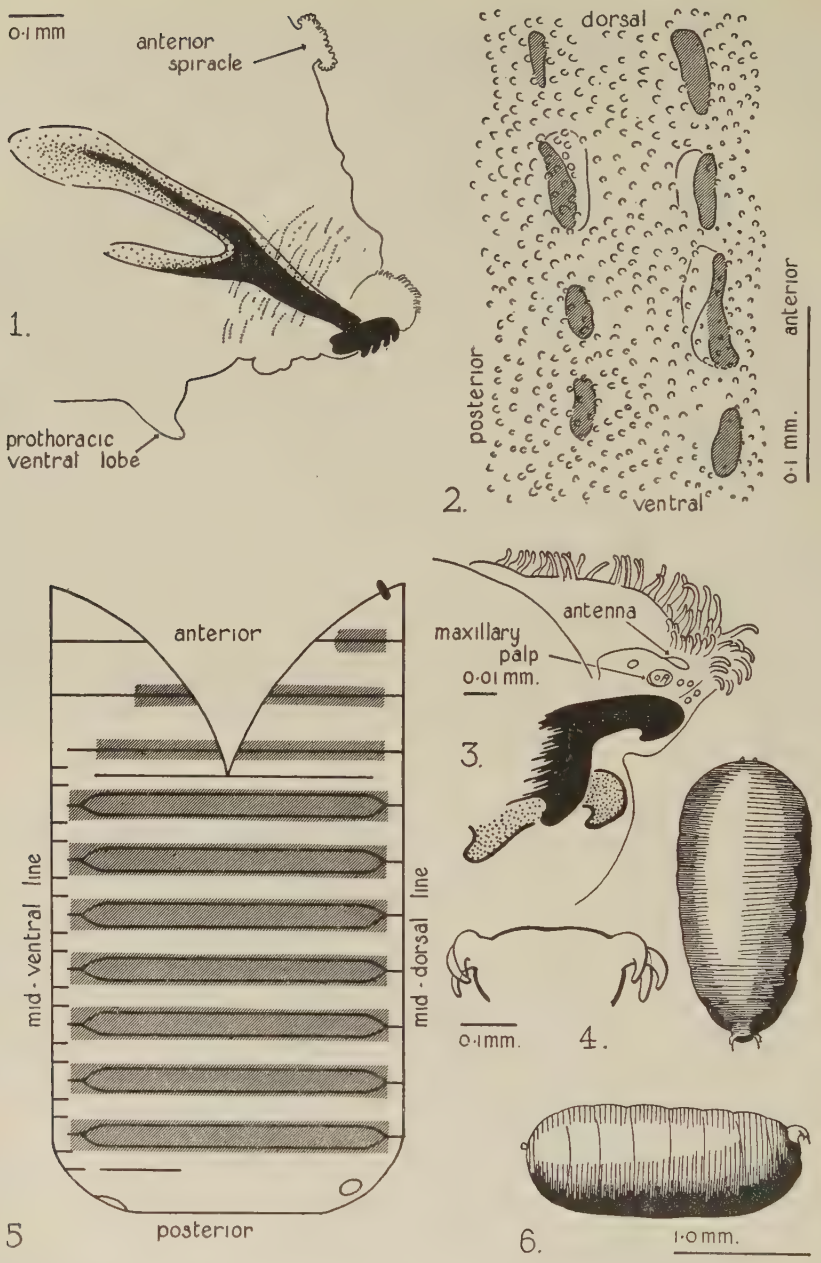

FIG. 1.—*Phytobia* (*Dizygomyza*) *iraeos* Goureau. (1) Anterior segments of larva. (2) Post-fourth abdominal tubercle band. (3) Facial mask. (4) Posterior spiracles of puparium. (5) Muscle scar and tubercle band patterns. (6) Puparium.

The anterior spiracles are small and have about 19 bulbs. The hind spiracles are raised on an eminence at the posterior end of the puparium and have each three horns directed downwards.

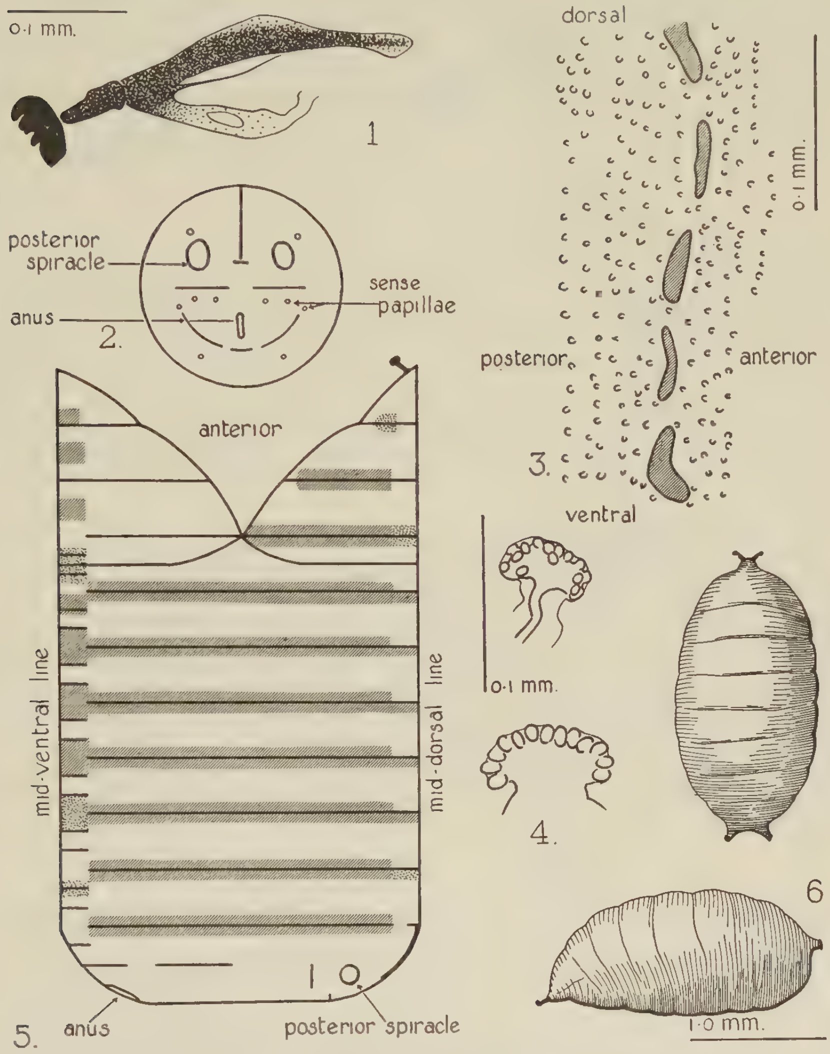

FIG. 2.—*Phytagromyza heringi* Hendel. (1) Mouthparts. (2) Posterior sense papillae. (3) Tubercle band. (4) Anterior and posterior spiracles. (5) Pattern diagram. (6) Puparium.

The mandibles have each two equal sized teeth and the right mandible is the larger, so that the teeth alternate. The labial sclerite appears continuous with the paraclypeal phragma, which consists of the upper arm of the dorsal process with a slight dorsal angle far forward, and the ventral process, which is about half the size of the dorsal and has no foramina. There are no longitudinal, lateral or anterolateral sclerites.

The head region immediately above the mandibles bears the maxillary palps and antennae, and probably at least three sense papillae on either side. On the mid-dorsal line are many long processes, most of them curved at the tip, and a few rows of small tubercles are found at the side of the head. On the prothorax there is a single ventral lobe.

It was not possible to see the sense papillae of the body segments or posterior end.

De Meijere (1925) described this species as *Dizygomyza morosa* Mg.

Phytagromyza heringi Hendel (Fig. 2)

This species mines the leaves of *Fraxinus excelsior* L. and was collected beside Loch Long, Dunbartonshire, Scotland. Pupation occurs within the mine. The puparium is brown, smooth and shiny, but with intersegmental grooves. The circular emergence fracture is in the first abdominal segment.

Muscle scars are transversely elongate, and the tubercles are medium sized. In the tubercle bands, which may be up to 48 per cent. of the lateral segment width, the arrangement of tubercles appears in places to be more or less in rows, but in other parts they are irregularly scattered. It should be noted that in the mid-dorsal line the tubercle bands lie only posterior to the muscle scar bands.

The anterior spiracles are stalked—this is especially noticeable in the puparium—and have about 15 bulbs. The posterior have about 13 in specimens which I have examined, and de Meijere (1938) records about 20.

The mandibles have each two teeth of similar size, and the right mandible is larger so that the teeth alternate. The labial sclerite is quite short and the suture not very conspicuous. The dorsal process, like that of *Phytomyza* species, is composed mainly of the upper arm, and the lower arm is much reduced; the ventral process is pale and foramina are present.

Sense papillae of the body segments are difficult to see, but those of the posterior segment are shown (fig. 2 (2)). Few larvae were found so that the facial mask was not examined.

Napomyza lateralis (Fallén) (Fig. 3)

The following description is from larvae and puparia from *Anthriscus sylvestris* (L.) Bernh. collected at Sunninghill, Berks.

The puparium is straw-coloured with darker brown spiracles and a smooth surface, only occasionally wrinkled in the anal region. A white line may be visible on either side at the anterior end formed by the larval longitudinal trachea coming into contact with the wall of the puparium. The annular emergence fracture is in the metathorax.

Muscle scars are frequently elongated anteroposteriorly and form undulating bands. Tubercles are very small and irregularly scattered in bands occupying less than 25 per cent. of the lateral segment width.

The spiracles are short and rounded with bulbs closely set in a double row which makes estimation of numbers difficult. De Meijere (1926) gives their number as about 10 and about 16 for anterior and posterior spiracles respectively. My specimens gave counts of about 16 and 20–22 respectively.

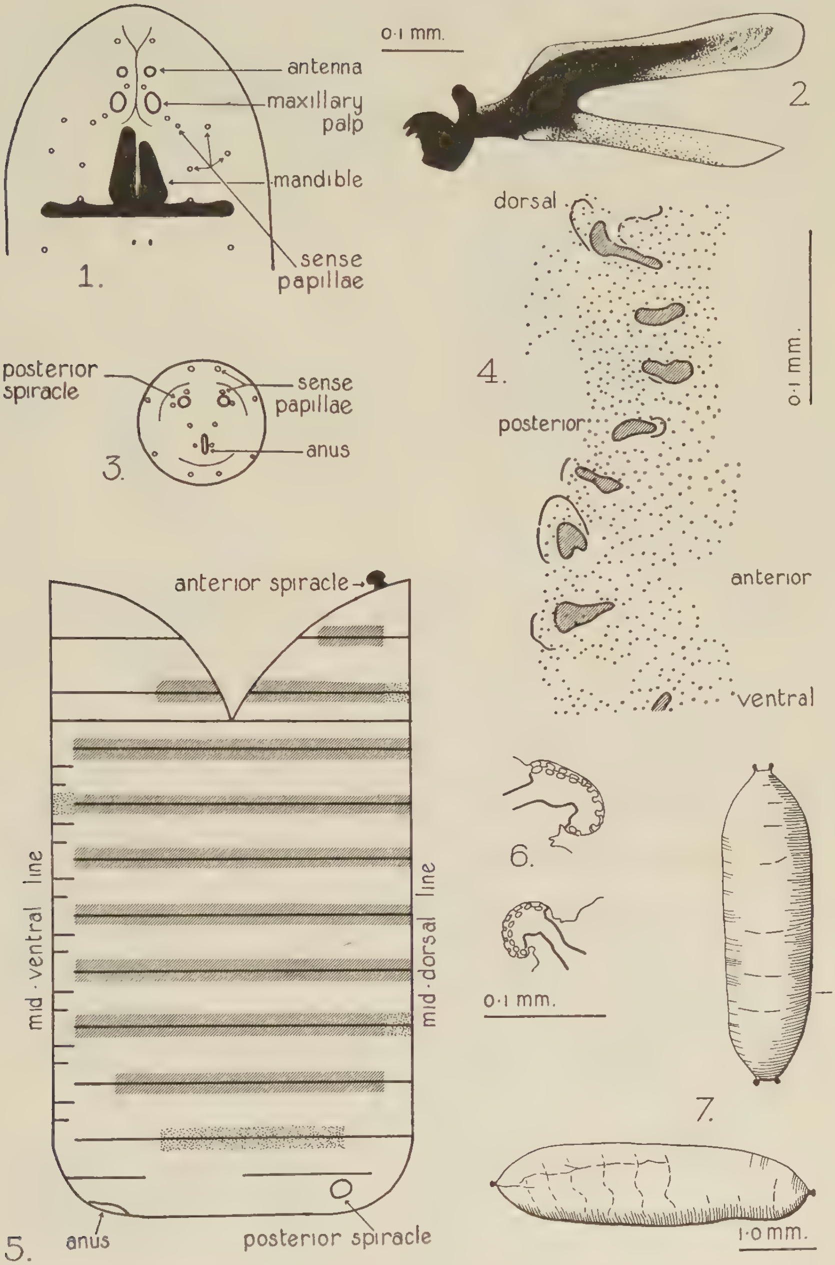

FIG. 3.—*Napomyza lateralis* (Fallén). (1) Facial mask. (2) Mouthparts. (3) Posterior sense papillae. (4) Tubercle band. (5) Pattern diagram. (6) Anterior and posterior spiracles. (7) Puparium.

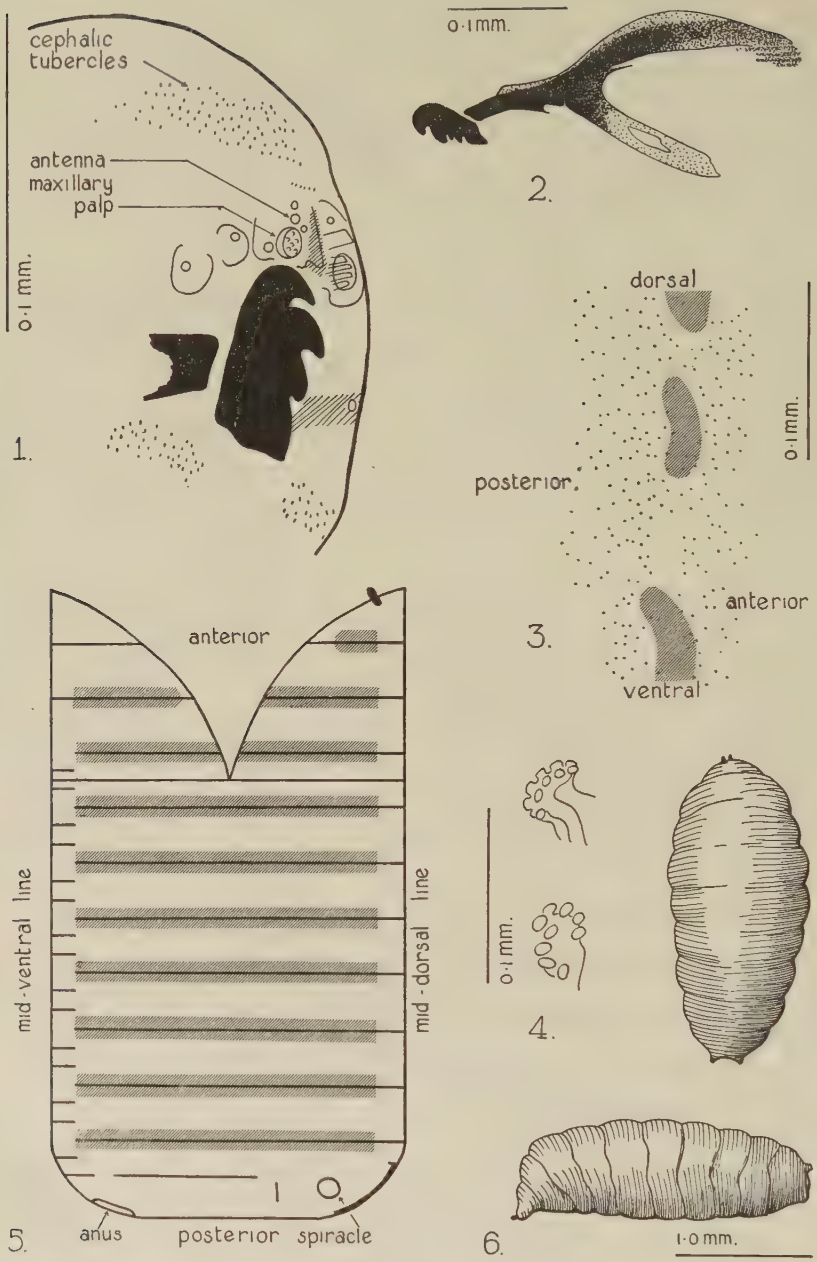

Fig. 4.—*Phytomyza atricornis* Meigen. (1) Larval head segment. (2) Mouthparts. (3) Tubercle band. (4) Anterior and posterior spiracles. (5) Pattern diagram. (6) Puparium.

The mandibles are compact and strong and each bears two teeth, the second tooth of the left mandible much smaller than the first, but those of the right mandible subequal. The right mandible is larger so that the bigger teeth form a triangle instead of alternating as do those of *Phytomyza* species. The labial sclerite is short and there is no suture visible between it and the paraclypeal phragma. The lower arm of the dorsal process is absent and the dorsal angle is well forward. The ventral process is paler and has no foramina. The lateral sclerites are well developed but the longitudinal and anterolateral are absent.

Sense papillae on the body segments usually number about 16 in a ring round the middle of the segment. Those on the eighth abdominal segment and on the facial mask form the patterns shown (fig. 3 (3) and (1)).

Phytomyza atricornis Meigen (Fig. 4)

This is a polyphagous species but my specimens were all obtained from Michaelmas Daisy (*Aster* sp.) at Belfast, N. Ireland.

The puparium is brown, fairly smooth and shiny, but with deep intersegmental grooves. The circular emergence fracture is in the first abdominal segment.

Muscle scars are transversely elongate but are pale and difficult to see. The tubercle bands occupy only up to 30 per cent. of the lateral segment width, and are composed of very fine tubercles irregularly scattered Tubercles are found also on the head segment in two areas ventral to the mouth and one dorsal band.

The spiracles are small and it is difficult to count the exact number of bulbs ; the anterior spiracles had about 10–12, and the posterior 8–10 ; de Meijere (1926) mentions 6–10 and 6–9 respectively.

Mouthparts and cephalopharyngeal apparatus are of the typical *Phytomyza* type, the right mandible being larger, the lower arm of the dorsal process reduced, and foramina present in the ventral process.

Sense papillae are difficult to see in the puparium and could not be counted. Sense papillae of the facial mask are shown (fig. 4 (1)) and it will be seen that the longitudinal and lateral sclerites are extremely pale.

Phytomyza minuscula Goureau (Fig. 5)

Only puparia of this species were obtained from Columbine (*Aquilegia* sp.) at Belfast, N. Ireland.

The puparium is brown, smooth and shiny, and pupation takes place outside the mine. The circular emergence fracture is in the first abdominal segment.

Muscle scars are oval, transversely elongate. Tubercle bands may be up to 48 per cent. of the lateral segment width and the tubercles are quite small and irregularly scattered. A patch of tubercles frequently occurs on the posterior segment below the subspiracular muscle group.

The spiracles of the puparium are very small ; de Meijere (1934) gives counts of about 9 and about 14 bulbs respectively.

The mouthparts are of the typical *Phytomyza* type, but those in the puparia were always found spread flat on the ventral surface and thus did not present the appearance of normal larval mouthparts.

Sense papillae on the body are too pale to distinguish in the puparium, and as no larvae were obtained the facial mask could not be examined.

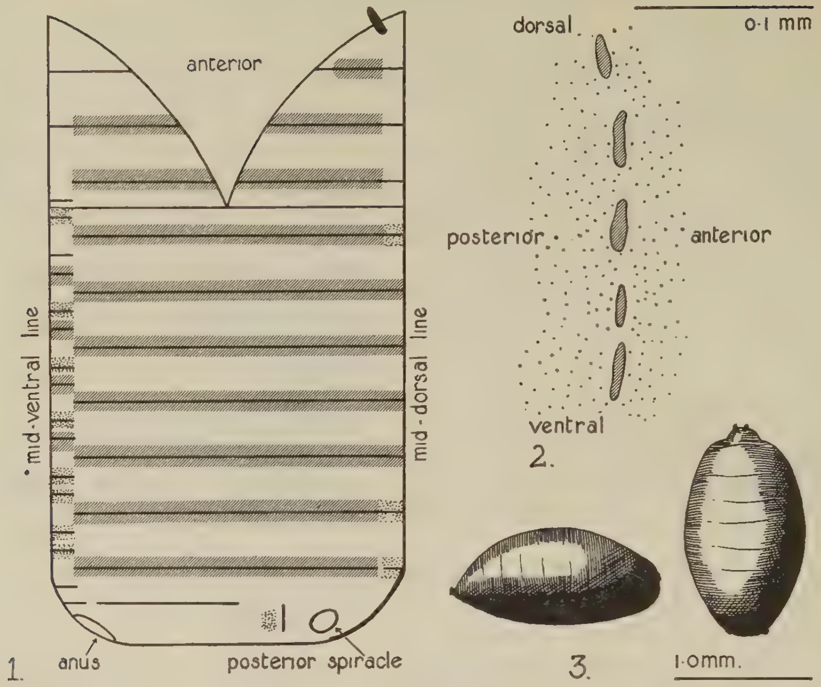

Fig. 5.—*Phytomyza minuscula* Goureau. (1) Pattern diagram. (2) Tubercle band. (3) Puparium.

Melanagromyza sp. (Fig. 6)

This species was collected from stems of wild *Pastinaca sativa* L. from Bibury, Gloucestershire. It was then identified as *M. aeneiventris* (Fallén) but the genus is at present undergoing revision.

The puparium is pale yellow with darker spiracles, the posterior spiracles usually separated by more than their transverse diameter. These spiracles are circular with an almost complete ring of 11–13 bulbs and a projecting tooth in the centre, which is often broken at the tip. The anterior spiracles are short and rounded with two rows of sessile bulbs—about 14–15. The annular emergence fracture lies in the metathorax ventrally and in the first abdominal segment dorsally and there is a mid-dorsal fracture separating the anterior spiracles in addition to the usual lateral fracture.

The muscle scars are elongated anteroposteriorly. Tubercles are large and rounded and scattered in bands which may occupy up to 50 per cent. of the lateral segment width.

The mandibles are very dark, with the left mandible larger, and each has a large apical bluntly rounded tooth and a smaller second tooth. The labial sclerite is short and distinctly separated from the paraclypeal phragma by a suture. The dorsal and ventral processes are subequal and the dorsal is composed of a broad lower arm and a narrower upper arm. There are no foramina in the ventral process. Anterolateral sclerites and small laterals are present.

The pattern of sense papillae on the facial mask and the posterior segment are shown (fig. 6 (1) and (3)).

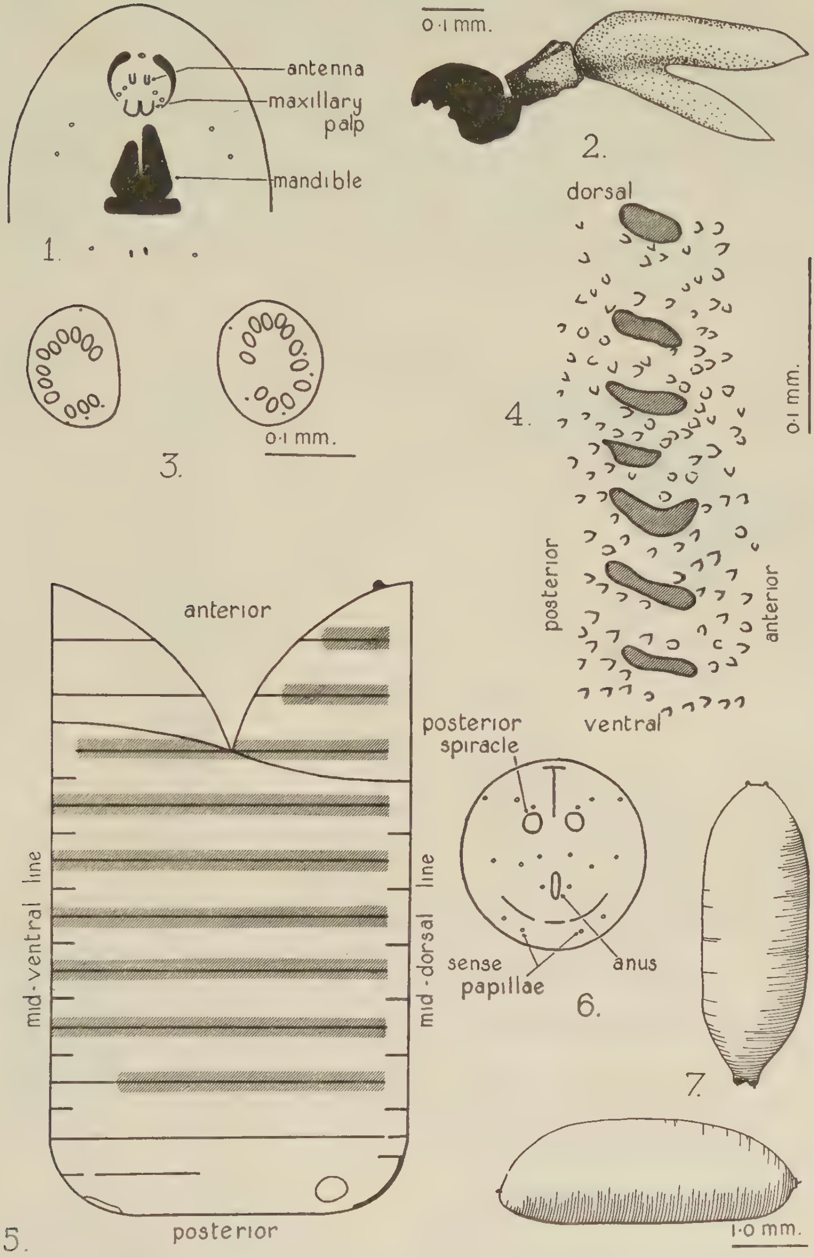

FIG. 6.—*Melanagromyza* sp. (1) Facial mask. (2) Mouthparts. (3) Posterior spiracles. (4) Tubercle band. (5) Pattern diagram. (6) Posterior sense papillae. (7) Puparium.

De Meijere (1925) refers to the species *aeneiventris* as having about 18 bulbs in the posterior spiracles, or 13–17 on *Cirsium* as a food plant. He describes it also as having " sehr klein " tubercles, which I did not find to be so. However, de Meijere's material was not from *Pastinaca sativa* and it may be that more than one species is involved.

In a species of *Melanagromyza* which I collected from *Angelica sylvestris* L. and *Heracleum sphondylium* L. at Sunninghill, Berks., and identified as *M. lappae* Lw., the muscle scar and tubercle band patterns, and the facial mask and posterior segment sense papillae appeared identical with the above description. The difference lay in the slightly larger size, the approximation of the posterior spiracles, and the larger lateral sclerites of this second species.

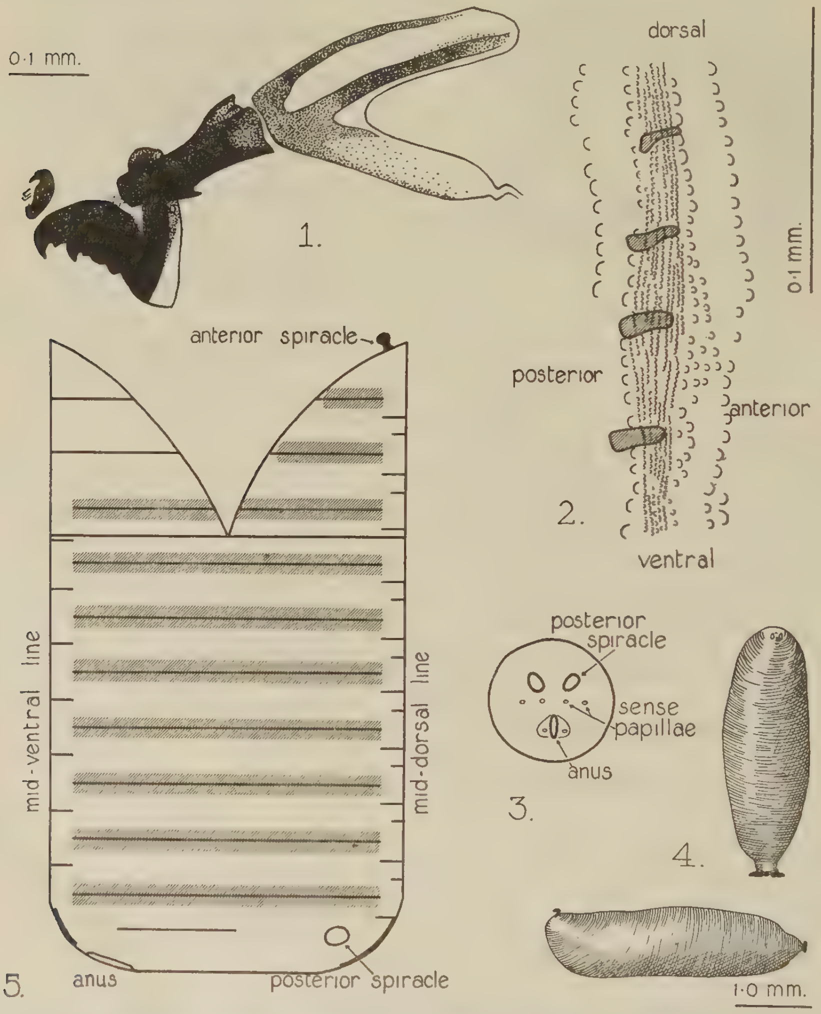

Fig. 7.—*Ophiomyia heracleivora* Spencer. (1) Mouthparts. (2) Tubercle band. (3) Posterior sense papillae. (4) Puparium. (5) Pattern diagram.

Ophiomyia heracleivora Spencer (Fig. 7)

This species was collected from *Heracleum sphondylium* L. near Ascot, Berks. It was at first taken to be *O. maura* (Meigen), then the only species of this genus known to occur in Britain, and I have discussed it as such (1956 and 1957*a*). Mr. K. A. Spencer has recently examined the adults and considers it to be a new species, which he has described as *O. heracleivora* (Spencer, 1957).

The puparium is brownish-black, smooth, but not very shiny. The annular emergence fracture lies in the first abdominal segment, and there is usually a mid-dorsal fracture in addition to the lateral fractures.

Muscle scars are more or less quadrangular with long axes running anteroposteriorly. The tubercles are rounded at the tip and are of two sizes, a number of rows of small tubercles lying between a few broken rows of larger size. The tubercle bands are narrow, occupying only about 10 per cent. of the lateral segment width.

The anterior spiracles are one-horned and curved downward, and the posterior are two-horned, but the number of bulbs could not be counted in the contracted condition and no larvae were found.

The mandibles each bear two teeth of unequal size and it appears to be the left mandible which is the larger. There is a clearly visible suture separating the labial sclerite from the paraclypeal phragma. Both upper and lower arms of the dorsal process are present and the lower is slightly longer. There is no marked dorsal angle. The ventral process is large and has no foramina but a small upper branch is present. Lateral sclerites are strongly developed and have sense papillae at the posterior border. Anterolateral sclerites are also present.

There appear to be only six sense papillae on the posterior segment. Other body segments have 14–18 arranged in a midsegmental ring.

Agromyza sp. ? *johannae* de Meijere (Fig. 8)

Puparia were obtained from leaf-mines in *Sarothamnus scoparius* (L.) Wimmer at Belfast, N. Ireland, but no adults emerged to confirm the identification.

The puparia are brown, rough and ridged, with intersegmental indentations. Projections at the posterior end appear at first to be anal lobes but inspection reveals that they lie between the anus and the posterior spiracles. The circular emergence fracture lies in the first abdominal segment.

Muscle scars are rounded or oval, and the tubercles are large but the bands usually occupy less than 30 per cent. of the lateral segment width. The tubercles are irregularly scattered in the bands.

The spiracles are very contracted in the puparium and as no larvae were examined it was not possible to count the number of bulbs. For the same reason the facial mask was not examined ; sense papillae on the other segments of the body were difficult to see.

The mandibles appear to be of equal size and each bears two teeth. The suture between the labial sclerite and paraclypeal phragma is barely visible. The upper and lower arms of the dorsal process are both present, the former tapering to its extremity but the latter broad and slightly longer. The ventral process has no foramina, and there do not appear to be longitudinal, lateral, or anterolateral sclerites present.

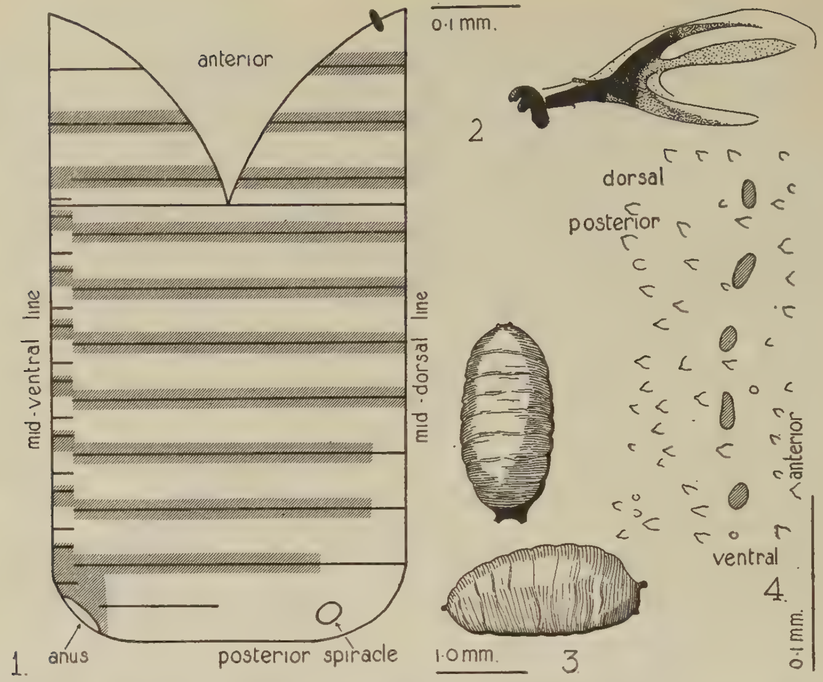

FIG. 8.—*Agromyza ? johannae* de Meijere. (1) Pattern diagram. (2) Mouthparts. (3) Puparium. (4) Tubercle band.

DISCUSSION

Comparison of the larval features of these representatives of several genera reveals a number of points of difference. Differences in tubercle distribution are probably of specific significance only but many other characters also vary.

Frick (1952) has already given a key to genera using the larval mouthparts. It will be noticed, however, that certain features not mentioned by him may be important. In the representatives of the Phytomyzinae—*Phytobia*, *Phytagromyza*, *Phytomyza*, and *Napomyza*—it is the right mandible which is the larger, whereas in those of the Agromyzinae—*Agromyza*, *Melanagromyza* and *Ophiomyia*—the mandibles are equal in size, or the left one is larger.

Frick's separation of the subfamilies on the relative sizes of the upper and lower arms of the dorsal process is confirmed by examination of the above species—Agromyzinae have both arms well developed, and the lower is slightly longer, but in Phytomyzinae the lower arm is reduced or absent.

The occurrence of lateral and anterolateral sclerites may also prove important in separating different genera, although not connected with the division into subfamilies.

Frick discusses the phylogenetic relationships of the genera on the evidence of adult external morphology and male terminalia. However, in the above species at least, the mouthparts of *Phytomyza* and *Phytagromyza* seem very much more alike than those of *Phytomyza* and *Napomyza* which are near neighbours on Frick's phylogenetic tree. This difference shows also in the pattern of muscle scars and in the fact that *Napomyza* has a metathoracic emergence fracture.

Comparison of the muscle scar patterns of the other species shows that *Agromyza* also has a pattern similar to that of *Phytomyza* and *Phytagromyza.* The representatives of the other genera each have individual patterns, easily separable.

It is not desirable to generalise from single examples of each genus, and it remains for future investigations to show whether the muscle scar patterns are diagnostic for a genus, as the evidence of *Phytomyza* species already studied seems to indicate. Further work on the distribution of sense papillae, both facial and posterior, would be interesting.

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BOOK NOTICE

The Nigerian Butterflies. Pt. 1. *Papilionidae.* By J. BOORMAN and P. ROCHE. 8vo. Ibadan (University Press), 1957. Pp. 15 : 31 pls. 10*s.*

This is the first work in a series dealing with the butterflies of Nigeria, which is to be published in nine parts.

It is designed to help the casual observer identify the species occurring in Nigeria and the British Cameroons and will be useful to both the specialist and amateur.

This part, conforming to the general plan of the series, consists mainly of life-size black and white photographs. Where there are marked differences between the sexes both are shown, and also the undersides of the wings when this is important to identification.

The text is kept to a minimum and consists of brief descriptions of each plate giving colours and habitat.

In the present part 30 out of the 33 species of Papilionidae known to occur in the country are illustrated.

THE OVIPOSITION BEHAVIOUR OF *ACHROIA GRISELLA* (FABRICIUS) (LEPIDOPTERA : GALLERIIDAE)

By P. Makings

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Recent investigations of the oviposition behaviour of Lepidoptera (Makings, 1956*b*) included studies on *Achroia grisella* (Fab.). A variety of observations and experiments revealed a fairly clear picture of the oviposition requirements and behaviour of this species. The results have also suggested some conclusions on the nature of the oviposition behaviour, which appear to be of wider application.

The insects were cultured in a constant temperature room at 25° C. and 75 per cent. Relative Humidity. At first they were bred on the natural medium —old wax brood-comb from beehives. As this material was not readily available, the artificial medium devised for *Galleria mellonella* (L.) by Haydak (1936) was tried. This material tended to become sticky, drowning eggs and larvae, but it was found that, if the mixture was allowed to stand for a week after being made up, the fluid ingredients dispersed thoroughly so that the medium was of a fairly dry consistency. It was then broken up into a granular form and well mixed with rather more than its own volume of sterilised (oven-dried) peat, which absorbed the excess fluid which exuded from it. An important additional advantage was that the structure of the peat proved suitable for the reception of eggs and obviated the necessity for providing any special material for oviposition. The results obtained with this mixture were extremely satisfactory, and the method can be highly recommended. It was not found necessary to provide food for the adults in cultures or experiments.

The behaviour described in this paper is that of the fertilised female. Virgin females show a similar behaviour pattern. Terms describing behaviour are used with the meanings defined in the paper by Thorpe (1951). The entomological nomenclature follows Kloet and Hincks (1945).

The Oviposition Site

The natural oviposition site of this species is not known, although it is believed that the female lays its eggs inside the hive, so that any attempt to find eggs would require the destruction of hives. It was therefore decided to offer likely materials under experimental conditions.

Preliminary observations showed that the females will lay their eggs in cracks in the fabric of cages ; it was therefore necessary to use glass containers with the minimum of joints and angles. Large glass dishes, covered by a sheet of glass, were used and the various materials were placed on the bottom of the dish. The materials used and the results obtained are shown in Table I.

Since the larvae normally feed on the wax comb (Beirne, 1952) it might be expected that it would be attractive to the ovipositing females. In fact, the

Table I.—*Selection of oviposition sites by* A. grisella (*Fab.*)

		Oviposition sites	Total of 5 experiments, 2 moths in each (No. of eggs per site)	Total of 2 experiments, 15 moths in each (overcrowded) (No. of eggs per site)
Materials present in the dish	A	Crevices on bark	0	92
		Wax comb	0	0
		Rough wooden block (surface)	0	1
		Exposed xylem vessels of wood	11	14
		Crevice between wood and glass	0	359
		Glass surface	4	1
		Total	15	467
	B	Crevices on bark	0	2
		Wax comb	0	0
		Rough wooden block (surface)	0	2
		Exposed xylem vessels of wood	10	27
		Crevice between wood and glass	77	282
		Glass surface	0	0
		Total	87	313
		Total in crevices	98	776
		Total on surfaces	4	4

In each experiment the materials were present both separated from each other (A) and in a group (B).

comb itself was not selected, the most favoured place being the deep crevice between a small block of wood and the glass floor. Shallow crevices were much less attractive and flat exposed surfaces carried only eight of nearly a thousand eggs. This crevice-selecting habit may serve to protect the eggs from the mandibles of the bees. The absence of eggs on the comb used in the experiments may be partly explained by this habit although, as will be shown later, other factors are involved. The comb used was cut from an undamaged piece and provided no crevice. Although eggs were not laid on the wax, it seemed clear that it was " attractive " to the moths, since the crevices in which most eggs were laid were in a group of materials which included wax. Similar crevices without wax contained few eggs, except under overcrowded conditions when all the crevices were filled. The eggs were usually compressed and somewhat distorted when deposited in narrow crevices. The viability was unaffected as virtually every egg hatched, an unusual occurrence in the Lepidoptera. If crevices are freely available, *A. grisella* females seldom lay eggs in those of sufficient width to avoid any compression. They are usually laid, not singly, but in fairly large batches; Table II shows a typical result of counting the number of eggs in a series of batches. For this purpose a batch is defined as either a single egg or a group in which each egg touches one or more of the others.

TABLE II.—*The number of eggs in each batch of a typical series. Arranged in order of size*

1	2	14	22	32	58
1	2	14	22	34	64
1	3	16	23	42	65
1	4	18	26	42	67
1	8	18	27	47	67
1	10	19	28	48	67
1	11	20	28	48	77
1	12	20	31	49	83
1	13	20	31	54	90
2	13	20	31	55	114

These preliminary experiments therefore show that the eggs are laid in batches in narrow crevices near beeswax but not necessarily in contact with the wax itself. The crevices are nearly always so narrow as to cause distortion of the eggs but this does not reduce their viability. These facts formed the basis of analytical experiments and observations on the behaviour of the moths. The factors to which most attention was given were olfactory and tactile.

THE RESPONSE TO OLFACTORY FACTORS

Previous workers have concentrated on the chemical aspects of host-material selection, and in some cases the effectiveness of specific odours in stimulating oviposition is beyond question (Knoll, 1921; and others). It is not so clear whether ovipositing females are attracted from a distance by odour. The effect may be to stimulate oviposition when such a female is close to the source of the odour. " Attractant " and " stimulant " are defined as follows: an attractant is a factor which induces the insect, at some distance from the source, to orientate to and move towards the source; a stimulant is a factor which induces any other form of response. Clearly, attraction is only a particular type of stimulation, but it is useful to have this special distinction in discussing the effects of olfactory factors. Many day-flying species are first attracted to the host by sight and afterwards stimulated by olfaction (Ilse, 1937; Knoll, 1921). In such cases, the status of olfaction is clearly that of a stimulant, not an attractant. However, olfaction is generally regarded as the initial attraction in other cases, particularly in nocturnal species, where the initial attraction is not a visual one. Nevertheless, the general assumption that olfaction acts as an attraction to the female over any appreciable distance seems to be unjustified and was certainly not supported by the evidence obtained during the general investigation (Makings, 1956*b*). The behaviour of *Hypocrita jacobaeae* (L.) in the neighbourhood of the host-plant *Senecio jacobaea* (L.) indicates fairly clearly what actually happens and will be described elsewhere. The results obtained with *A. grisella* emphasise the importance of distinguishing between attracting and stimulating effects of an odour.

The usual type of olfactory " choice-chamber " apparatus was found to be unsuitable for *A. grisella* because of its habit of laying eggs in cracks in the construction and a special type of apparatus was therefore constructed. This may be called the " slide-block " apparatus, developed as a means of investigating crevice width preferences. In describing a crevice, three measurements are used, *viz.*: width (the distance between the two opposing faces which form the crevice), length (the distance along the aperture of the crevice, measured at right angles to the width) and depth (the distance from the aperture measured at right-angles to both the width and the length). The slide-block consists of a number of glass microscope slides, each separated by varying numbers of glass cover-slips at one end, to form crevices of different widths. In the case of batch-laying species such as *A. grisella*, the glass slides have the added advantage that the eggs may be counted simply by looking through the glass, whereas opaque material would need to be dismantled to do this. The block is held together by rubber bands. For olfactory experiments with *A. grisella*, melted wax was dropped on to a glass slide and another slide pressed on it to produce a suitable crevice. It was necessary to use these blocks in large petri dishes to avoid forming extraneous crevices, but Table III shows that a response was obtained in spite of the enclosed nature of the apparatus. As the moths could in no way touch the wax, the response must be an olfactory one.

TABLE III.—*The response of* A. grisella (*Fab.*) *to beeswax*

Type of experiment	No. of experiments	In crevice with wax	In crevice with no wax
Test. Using entire moths .	4	251	97
Control. No wax in either block	4	108	116
Test. Using moths with the antennae removed . .	8	237	247

The experiments with moths after removal of the antennae[1] indicate that these organs alone are responsible for the response. Slifer (1956) similarly found that the response of certain grasshoppers to the odour of food was dependent solely on the antennae.

The results given in Table III appear to indicate that the ovipositing females are " attracted " by the wax, but further experiments showed that, as suggested earlier, its effect is actually one of stimulation rather than attraction. Moths in the " ready to lay " condition were placed in a petri dish with a spot of wax dropped on the bottom so that it formed a tiny dome which produced no crevice of any kind. The moths did not congregate near the wax, as might have been expected if it were attractive, nor did they pause near it, but walked about the dish and even over the wax spot, exhibiting the characteristic probing action of the ovipositor from time to time. The positions of the eggs which were eventually laid singly on the smooth surface bore no relation to the position of the wax spot, but were distributed evenly over the dish. The results in Table III show that the olfactory effect occurs and is not obscured by enclosure in the dish so that it may be concluded that there is a response to the wax which is not directed to the wax itself but consists of a stimulation to oviposition. When crevices are available with and without wax, those with wax are used. There is thus an apparent olfactory preference effected by this mechanism.[2] The data in Table IV support this view as they show that, in a given period, more eggs are laid in a smooth dish containing wax spots than in a similar dish with no wax, and also that more eggs are laid in crevices if the odour of wax is present than if the odour is absent.

[1] This technique is discussed by Wigglesworth and Gillett (1934).

[2] See also page 145.

Table IV.—*Numbers of eggs laid by* A. grisella (*Fab.*) *in* 24 *hours under various factorial conditions*

Conditions of experiment	Number of moths used (each in a separate experiment)	Average number of eggs per moth
Neither wax nor crevice present	18	0·33
Only wax present	6	28·5
Only crevices present	36	32·1
Both wax and crevices present	10	34·9

The Response to Tactile Factors

The crevice width preferred by *A. grisella* for oviposition was determined by means of the slide-block technique already described. The eggs were laid in batches in the slide-block crevices and the width of the crevice at the point of oviposition was measured, using a micrometer eyepiece fitted to the microscope. The results are shown in Table V.

Table V.—*Selection of crevice width for oviposition by* A. grisella (*Fab.*)

Expt. No.		Aperture width with number of eggs (aperture width in μ)													
1	Width	128	128	128	138	138	165	174	183	193	193	211	339		
	Eggs	1	2	1	1	20	90	18	77	67	23	42	22		
2	Width	128	147	183	211										
	Eggs	20	34	67	22										
3	Width	119	128	138	147	147	165	174	174	193	193	219	266		
	Eggs	1	4	8	1	65	14	3	2	20	31	114	48		
4	Width	147	155	165	165	174	219	219							
	Eggs	2	83	54	31	1	32	10							
5	Width	201	238	248											
	Eggs	64	48	47											
6	Width	165	174	201	201	211	229	229	266						
	Eggs	42	11	19	49	18	55	31	67						
7	Width	64	110	128	138	155	155	165	165	183	183	201	211	238	238
	Eggs	14	1	1	12	16	1	58	26	27	28	13	28	13	20

Five females were used in each experiment.

The crevice-width preference of the females was indicated by plotting the number of eggs in each width range in the form of a histogram, as shown in figure 1. It is clear that this species is highly selective in the matter of crevice width, the choice being made between strikingly narrow limits. The same was found to be true for *Ephestia kühniella* Zeller and certain other " crevice-choosing " species. The preferred width for *A. grisella* is between 0·15 and 0·20 mm. The limits are 0·05 and 0·35 mm., but over 75 per cent. of the eggs were laid in the range 0·15–0·25 mm. It may be noted that figure 1 indicates that the moths are able to discriminate between crevice widths which differ by as little as 0·05 mm. from the optimum for the species. It seemed most likely that the selection was effected by each moth using a crevice into which the ovipositor would just fit. This theory was tested by determining the preferred crevice size for each individual moth and then comparing it with the measured width of the ovipositor tip. This experiment was not easy and only successfully accomplished with three moths (Table VI). It will be seen that the correlation in these three is remarkable.

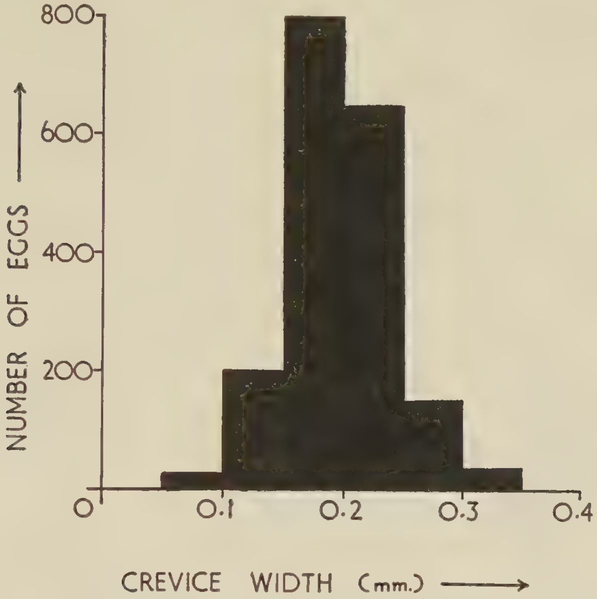

Fig. 1.—Histogram showing the crevice width preferred for oviposition by *A. grisella.*

Table VI.—*Comparison of width of the ovipositor tip with the preferred crevice width, for three individuals of* A. grisella (*Fab.*)

Female No.	Preferred crevice-width $= \frac{\text{sum of (width} \times \text{eggs)}}{\text{Total eggs}}$ (in mm.)	Width of the ovipositor tip (in mm.)
1 . . .	0·20	0·19
2 . . .	0·18	0·17
3 . . .	0·21	0·20

In Table VII the average measurement of eleven other specimens is compared with the preferred crevice width of the species as determined from the figures in Table V. Similar results for other species are also shown.

The depth of the crevices provided in these experiments was greater than the length of the extended ovipositor and it was noticed that the egg batches laid were at a more or less uniform distance from the aperture of the crevices. Most of the eggs were apparently inserted as far as the ovipositor could penetrate. Experiments on *E. kühniella* showed that a deep crevice is preferred to a

TABLE VII.—*Comparison of width of the ovipositor tip with the preferred crevice width, for four species of Lepidoptera*

Species	Preferred crevice-width (in mm.)	Average of measurements of ovipositors (in mm.)	No. of specimens measured
A. grisella (Fab.)	0·19	0·20	11
Ephestia kühniella Zeller	0·21	0·22	5
Aphomia sociella (L.)	0·28	0·24	1
Chesias legatella (Schiff.)	0·56	0·41	2

shallow one which would provide an apical stimulus to the ovipositor but not allow maximum penetration. It might be supposed that the preference for deep insertion is induced merely by its effect of increasing the stimulus to the sides of the ovipositor. Examination of extended ovipositors showed that a band of setae occurs on the eighth tergal plate, which forms the proximal part (Eidmann, 1929). If these setae were stimulated by contact with the edge of the crevice, their position would account for the deep insertion response. Figure 2 shows the ovipositor of *A. grisella* (this specimen was chosen because it also shows the act of extruding an egg); the setal band, which is similar to that of *E. kühniella*, is particularly well shown. When the ovipositor is retracted these setae are folded flat and hidden, but they stand erect, as shown in figure 2, when it is extended. The possibility that the setal band was responsible for the regulation of the depth of insertion of eggs could not be tested by direct observation, nor was it possible to damage the setae. Circumstantial evidence was obtained, however, by comparing measurements of the depth of insertion of eggs with measurements of the distance from the setal band to the tip of the extended ovipositor. The results are given in Table VIII.

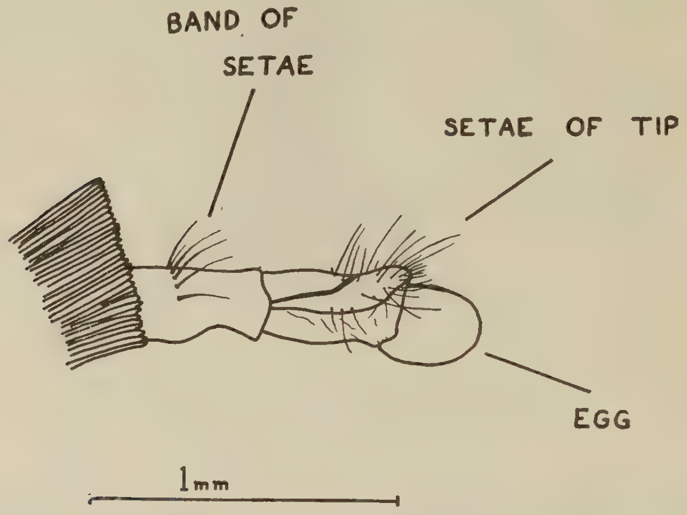

FIG. 2.—Ovipositor of *A. grisella*. Left lateral view. (The specimen is partly extended and in the act of extruding an egg.)

TABLE VIII.—*Comparison of the depth of insertion of eggs in crevices with the distance from ovipositor tip to the setal band, for* A. grisella (*Fab.*)

Distance from crevice aperture to inner-most egg (in mm.)	Distance from setal band to tip of extended ovipositor (in mm.)
2·75	3·15
2·98	2·73
2·52	3·29
2·84	2·65
2·20	3·53
2·75	2·48
2·06	2·90
2·84	2·62
2·66	2·62
Mean = 2·62	Mean = 2·88

The innermost egg of a batch is the first laid and thus determines the crevice selection. Considering the difficulties, such as avoiding distortion when everting the ovipositors, the results seem to favour the hypothesis. Setae are also present in a similar position in many of the species which do not deposit their eggs in crevices (Pierce, 1952), but in these cases they are close to and grouped with the apical setae, whose functions they may share. It is possible that the function of the setal band is concerned with the movements of the ovipositor itself, particularly retraction, but it was not possible to test this by damaging the setae.

THE BEHAVIOUR PATTERN

In order to supplement the analytical study, attempts were made to observe the behaviour of females in experimental cages. *A. grisella* is crepuscular or nocturnal so that oviposition normally occurs in darkness, and experiments showed that any illumination suitable for observation usually inhibits activity. On the other hand, females kept under observation would occasionally become active during the day and walk about the cage exhibiting oviposition behaviour. Waloff and Richards (1946) showed that *Ephestia elutella* (Hübner) lays eggs throughout the 24 hours, but with a maximum (95·3 per cent.) at night, corresponding to the normal activity period. Probably the daytime " awakening " of *A. grisella* is of a similar nature. In such cases the inhibitory effect of light (and possibly other factors) was no doubt eventually overcome by the build-up of the unreleased oviposition " drive " produced by internal conditions. It was found that the best way was simply to record the oviposition behaviour of moths while under observation for any reason. Such opportunities, taken over a period of time, were enough to establish the normal pattern as it occurs in the laboratory. It was also noticed that females taken from the constant temperature room to the laboratory would often begin the oviposition behaviour. Experiments with *Diataraxia oleracea* (L.) in the constant temperature room indicated that the onset of the activity period was dependent on the onset of darkness. This was shown by means of a special aktograph (Makings, 1956*a*) which was unfortunately unsuitable for a moth as small as *A. grisella*. It may be suggested that the drop in temperature in the evenings normally supplements the light effect, and in the case of *A. grisella* taken from the constant temperature room the sudden drop in temperature initiated the activity. In the change from constant temperature room to laboratory the light effect was, of course, reversed and oviposition induced under such conditions was not normal. More emphasis was therefore placed on the observations of undisturbed moths.

At the commencement of oviposition behaviour, the moths became suddenly active and walked rapidly about the cage. There was very little flight, fewer than one in four of the observed individuals showing any flight activity. At most there were only a few short " hopping " flights in the early stages. This simple activity stage lasted between 2 and 15 minutes. No variation could be discerned in the antennal movement which accompanies all activity. In the next stage, the ovipositor was repeatedly protruded to contact the substrate while the moth continued walking rapidly. There was never any flight in this stage. Whenever a niche or crevice or similar variation in the surface was found by the ovipositor, the walking movement was immediately inhibited and a prolonged (up to five or ten seconds) probing response occurred. If the crevice was not found to be suitable, the walking activity was resumed. Ultimately a suitable crevice would be found and oviposition would follow. The probing stage between the initial activity and final oviposition was of very variable duration, lasting between about one minute and an hour. There was no indication of an approximate optimum period but it was noticed that the duration of each stage was proportional to the duration of the other ; thus a short activity period was followed by a short probing period. Hence the whole behaviour occupied from three or four minutes to over an hour. This suggests a connection between the duration of the behaviour period and the strength of the oviposition " drive ". This theory is supported by the fact that, although very many apparently suitable crevices were freely available, that finally selected for oviposition was seldom one of the first to be " found " by the moth and on at least one occasion the crevice eventually used by a moth under observation was one which it had previously " tried and rejected ".

The crevice finding and discrimination is apparently entirely dependent on the ovipositor. The " probing " occurs on any type of surface and the moths walk over rough and smooth surfaces in an apparently random manner, with no tendency to walk on any particular surface or area where crevices are present. Females in a dish containing a slide-block walked freely over the block with no tendency to remain on it. When the ovipositor encountered a crevice, the moth simply stopped walking, while the ovipositor probing continued. There was no obvious orientation.

The complete oviposition behaviour pattern was observed on about 20 occasions. The behaviour not followed by oviposition was also seen about the same number of times. Possibly this was due to insufficient " drive ", as most of these observations were made on moths in cages which contained no host material. Nevertheless, observations with such material present showed that the pattern was the same.

The small amount of flight is rather interesting. Waloff and Richards (1946) showed that *E. elutella* was most active in the evening and early morning and they also obtained females and eggs in jars of grain placed some yards from an infested warehouse. It seems probable that the females had flown that distance, so the lack of flight observed in *A. grisella* may have been partly due to the comparatively bright illumination of the laboratory.

DISCUSSION

Although the pattern of oviposition behaviour in *A. grisella* was found to be unaltered by the absence of the host material, the process was nevertheless delayed. Delay was also caused by absence of crevices. The effect of the absence of any one factor was to delay the behaviour until the " drive " carried it through to the next stage. Thus in the absence of crevices the initial activity would be repeated, halting each time after prolonged probing responses until ultimately the oviposition act would ensue. The eggs were then deposited singly and at random since the oviposition was forced by the " drive " in the absence of crevices. The reduced rate of oviposition caused by the absence of one or more factors has been illustrated in Table IV. The stimulatory effect of the wax is particularly clear from the results in this table. It may be noted that the possibility that the wax odour may induce a kinesis is not ruled out, although such an effect was not demonstrated. Nevertheless, if present, it would be limited to the second stage of the behaviour, when the ovipositor probing occurs. It has been shown that the wax odour stimulates the onset of this stage, so that whether or not a kinesis is also involved in no way alters the conclusions to be drawn from the results obtained.

The oviposition behaviour of *A. grisella* may be summarised as follows. The condition of readiness to lay initiates an activity period which includes the specific oviposition behaviour and normally terminates in the act of oviposition.

Results obtained with a number of other species of Lepidoptera showed that this was applicable to all. The details of the behaviour during the activity period vary with the species, but in each case the act of oviposition (whether of a single egg or a batch) is preceded by a period of special activity. The significance of this is that there is always a special pattern of behaviour during which the female becomes susceptible to the appropriate stimuli which guide the selection of an oviposition site. The stimuli for any one species are responded to in a definite sequence or response chain which ensures that the factors will, under normal conditions, lead to oviposition in a suitable site (Makings, 1956*b*). In the case of *A. grisella* the normal sequence is as follows. The condition of readiness to lay initiates an active " searching " phase. The odour of beeswax then initiates the probing period. Stimulation of the probing ovipositor arrests walking and stimulates further probing. Discovery of a crevice by entry of the ovipositor will lead to probing to test the crevice width and depth. Finally, a suitable crevice, providing the appropriate stimulation to the ovipositor, will stimulate oviposition.

Crombie (1941) showed that when the beetle *Rhizopertha dominica* (Fab.) was in an environment having the odour of food, the sense of touch became paramount in the selection of an oviposition site, with no continuation of the olfactory response. Crombie did not fully interpret his results in terms of a behaviour pattern, but it seems most likely that his results are due to a response-chain very similar to that described above. This is particularly interesting as *R. dominica* represents a different Order of insects, and it is suggested that the oviposition of many insects takes the form of a response-chain (see also Edwards, 1954).

The response-chain of *A. grisella* may be expressed diagrammatically as shown in figure 3. This also illustrates the way in which the oviposition " drive " may ultimately cause the behaviour to proceed along the sequence even in the absence of one or more factors, although there is then some delay and prolongation of the preceding stages. In such a case, of course, the oviposition site would be abnormal ; reference to figure 3 will show that, in the absence of wax, oviposition will eventually occur in any suitable crevice. However, if wax is available, but no crevices, it will stimulate oviposition but the absence of crevices will be inhibitory. In these circumstances, the earliest effect of the wax as an olfactory " attractant " will be nullified by the prolongation of the crevice-seeking stage and the resulting promiscuous oviposition.

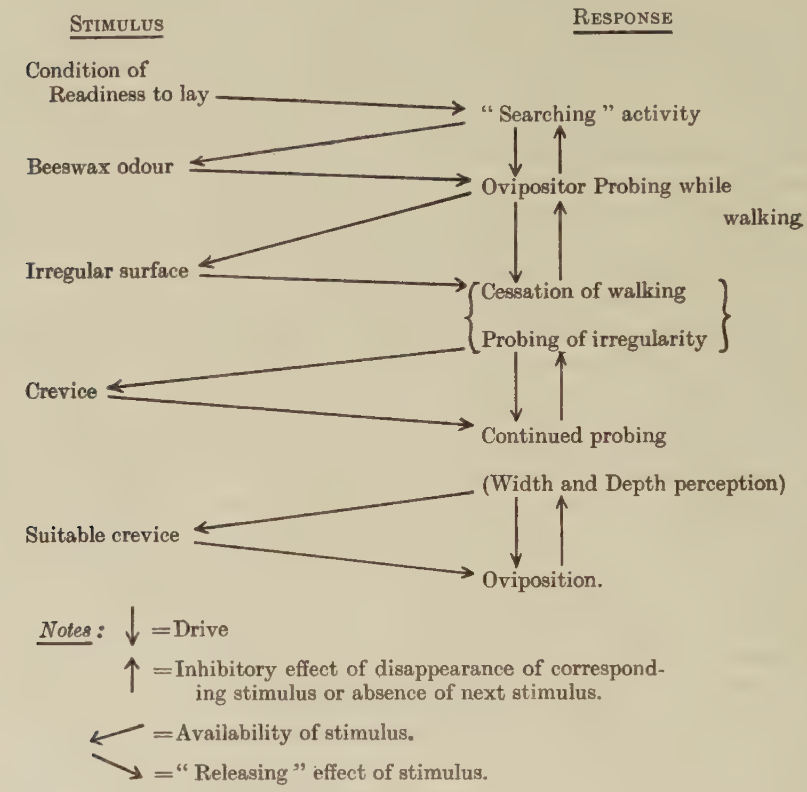
STIMULUS
RESPONSE
Condition of Readiness to lay
" Searching " activity
Beeswax odour
Ovipositor Probing while walking
Irregular surface
Cessation of walking
Probing of irregularity
Crevice
Continued probing
(Width and Depth perception)
Suitable crevice
Oviposition.
Notes :
= Drive
= Inhibitory effect of disappearance of corresponding stimulus or absence of next stimulus.
= Availability of stimulus.
= " Releasing " effect of stimulus.

FIG. 3.—Suggested oviposition behaviour response chain for *A. grisella.*

In this way, the elimination of one factor from the oviposition site can nullify the effects of factors which precede it in the response-chain and this may be of considerable significance in pest control. Thus the elimination of crevices in a beehive could not only make it unsuitable for oviposition by moths, but also nullify the olfactory " attraction " effect of the wax. This particular example may not be realized in practice, but similar measures may be very useful in the control of other pest insects when the details of the oviposition response-chains are known.

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SUMMARY

1. A new medium for culturing *Achroia grisella* Fabricius (Lepidoptera : Galleriidae) is described.

2. In the laboratory, the eggs are laid in batches in narrow crevices near beeswax but not necessarily in contact with the wax itself. The crevices chosen are so narrow as to cause distortion of the eggs but this does not reduce their viability.

3. A special type of apparatus is described for experiments on the ovipositional response to olfactory and tactile factors.

4. An ovipositional response to the odour of beeswax is demonstrated. The response is eliminated by removal of the antennae.

5. The effect of the odour of beeswax is shown to be one of stimulating oviposition rather than attraction of the females, using the terms stimulation and attraction with the meanings defined herein. The end result of the effect under normal conditions is to produce an olfactory selection which, however, should not be confused with attraction. This may also apply to other species.

6. The preferred crevice dimensions fall within narrow limits, determined by the morphology of the ovipositor, which is alone responsible for the crevice selection. This may also apply to other species.

7. The oviposition behaviour pattern is described and illustrated by a diagram. The arrangement of the behaviour into a response-chain probably applies, not only to other species of Lepidoptera, but also to other Orders of insects. The effects of this arrangement and their significance are discussed.

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BOOK NOTICE

Insect migration. By C. B. WILLIAMS. [The New Naturalist.] 8vo. London (Collins), 1958. Pp. xiii, 235 : 24 pls. (8 col.), maps, text-figs. 30*s*.

This work, which is the outcome of the author's lifelong interest in and study of the problem of insect migration, gives an up-to-date assessment of the present knowledge of the subject and discusses many of the problems raised.

The book is divided into four parts—Pt. 1, *The Introduction*, giving a brief history of the subject ; Pt. II, *The Evidence*, with chapters on the migration of butterflies, moths, locusts, dragonflies, ladybirds and other insects ; Pt. III, *Problems*, dealing with the nature of migratory flights, orientation and direction of flight ; the return flight ; geographical distribution ; and the relation of insect migrations to those of other animals ; and Pt. IV, *How the work is done*, giving information on the use of marked insects, collection and study of material, and books and publications on insect migration. An appendix gives details of immigrant butterflies and moths recorded in Britain each year between 1850 and 1955.

Though other volumes in the *New Naturalist* series are confined to the British Isles, the inclusion in the series of the present volume, extending far beyond these Islands, is justified since, as the editor points out, any book dealing generally with the problem of insect migration must be based on British material.

THE EFFECTS OF THE FLOODS OF 1953 ON THE AQUATIC INSECT FAUNA OF SPURN (YORKSHIRE)

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Introduction

The work here described was carried out in the boulder-clay area which comprises the south-eastern extremity of Yorkshire, between the North Sea and the Humber. A large part of this area was flooded by a high North Sea tide on 31st January–1st February, 1953 (Steers, 1953 ; Rossiter, 1954). The area had been studied every year since 1947, and its fauna prior to the flood was fairly well known. Sporadic collecting of aquatic animals from 1947 to 1951 was followed in July, 1952 by a systematic survey, in which the species found in each habitat were recorded. Salinities were measured by titration in the field against a standard solution of silver nitrate, and recorded as a percentage of North Sea water. (For details of the method *see* Hincks *et al.*, 1954 : 104.) The survey and salinity measurements were repeated in July each year after the flood until 1956. An account of the area and its aquatic habitats, together with a list of the pre-flood fauna and a preliminary report on the situation in 1953, has already been published (Hincks *et al.*, 1951–54).

General Effects of the Flooding

Before 1953 there were two rather sharply contrasted types of habitat, of low and high salinity respectively. The low-salinity habitats were not fresh : in 1952 they ranged from 3 to 15 per cent. sea-water. The largest of this group was Long Bank Dyke (LBD), which runs across the peninsula north of Kilnsea. In addition, the following ponds, all in Kilnsea Warren, were investigated: Pond in Marsh Meadow (PMM), Landmine Crater (LMC), Pond near Boundary Dyke (PBD), Bomb Crater in *Phragmites* area (BCP), Island Pond (IP), and a small pool in *Phragmites* area (PP). The most important of the high-salinity habitats was Walker Butts' Bank Dyke (WBB), near the Humber south of Kilnsea, which in 1952 had dried out to two small pools with a salinity of 81 per cent. South of Long Bank Dyke were a number of shallow saltings (SLB), in an area frequently flooded by the sea ; in 1952 these had dried out completely, except for one pool of 100 per cent. salinity. The high-salinity habitats contained much more water in wetter years, and their salinity must have fluctuated considerably. Boundary Dyke (BD) was saline at its western end, where it connected with WBB, and comparatively fresh at its eastern end. The low-

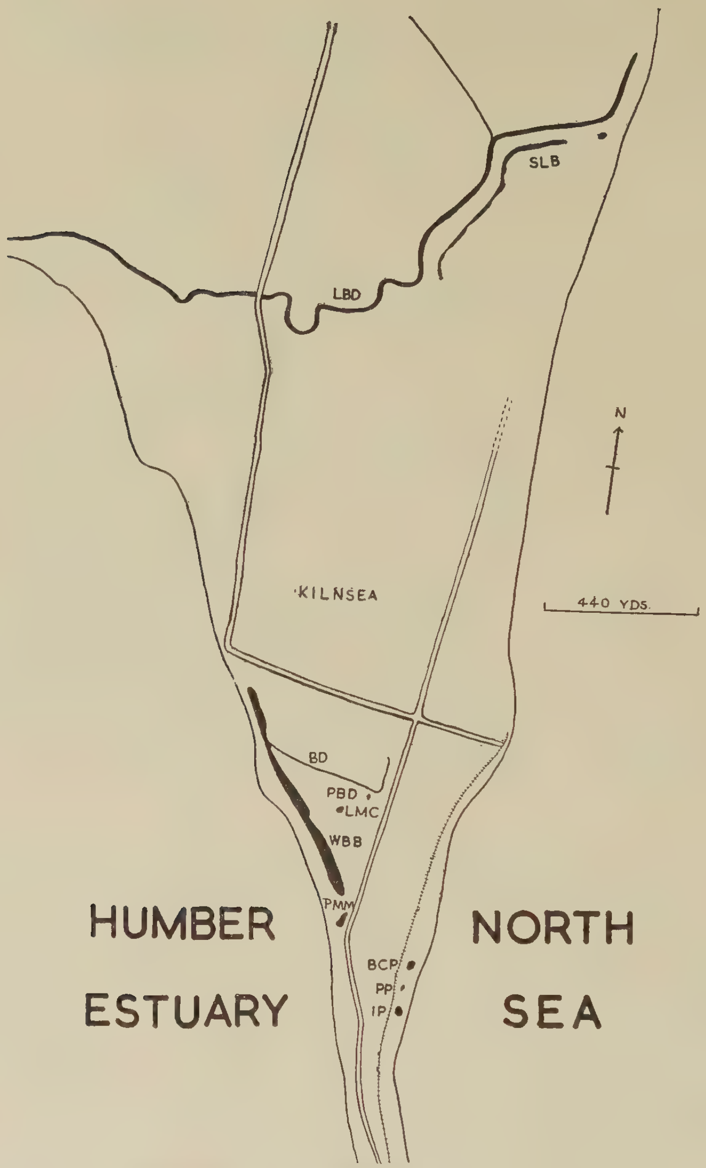

Fig. 1.—Map of Kilnsea area of Spurn Peninsula *BCP*, Bomb Crater in *Phragmites* area; *BD*, Boundary Dyke; *IP*, Island pond; *LBD*, Long Bank Dyke; *LMC*, Land Mine Crater; *PBD*, Pond near Boundary Dyke; *PMM*, Pond in Marsh Meadow; *PP*, *Phragmites* pond; *SLB*, Saltings near Long Bank Dyke; *WBB*, Walker Butt's Bank Dyke.

salinity habitats were characterised by *Ranunculus*, *Myriophyllum* and *Potamogeton*, the high-salinity habitats by *Ruppia*, *Zannichellia* and *Enteromorpha*. (For descriptions of the habitats *see* Hincks *et al.* (1951 : 84, 139ff. ; 1954 : 95.))

Flooding was most severe in the neighbourhood of Long Bank Dyke, where the land was covered to a depth of 5–6 feet. Kilnsea Warren was flooded to a depth of about 2 feet, mainly from the Humber. Water remained on low-lying ground for several days, and drainage was expedited by pumping from LBD and to a lesser extent from PMM. The salinities of the pre-flood low-salinity habitats rose considerably, and then declined till 1955. The rate of decline varied from habitat to habitat: in PMM the salinity had already fallen to 20 per cent. by July, 1953, but that of LMC, at the other extreme, was still 24 per cent. in 1955 (Table I). The rate of decline presumably depended upon the extent to which the habitat received rain-water drainage from the surrounding land. The pre-flood high-salinity habitats (WBB, SLB) were less affected by the flood. However, during the summer of 1953 WBB was re-dug and widened, and BD was cleaned out. Fragments of the original WBB remained in July, 1953, but the habitat had considerably changed in character by 1954. The salinity of the new dyke, together with that of the communicating BD, fell and in 1956 rose again, owing to the influx of Humber water through a culvert.

Table I.—*Salinities of habitats examined* (*percentage of sea water*)

Habitat	1952	1953	1954	1955	1956
PMM	3	20	7	3	2
LBD	5	24, 27	14	12	11–18
IP	14	43	19	6	8
BCP	10	60	23	8	11
LMC	5	73	50	24	24
PBD	5	40		Filled in	
PP	Dry	40	20	8	11
BD	5–100	7–29	3	Not examined	37–85
WBB	81	55, 57, 63	5	5	85
SLB	100	31, 56	Not examined		32, 40
New pools	.	28, 40, 43	.	.	.

As a result of the flooding, water of less than 20 per cent. salinity was practically eliminated from the area for the year 1953. By 1955 the pre-flood conditions had largely been restored, except that some of the formerly less saline habitats were still above 20 per cent., and WBB, which before 1953 had provided the richest fauna of the more saline habitats, was greatly impoverished by human action.

Summary of Results

The results from each annual visit are in the form of " species-habitat records ", denoting the finding of a species in a habitat of known salinity. Tables II–VI have been constructed from these raw data. Diptera and Trichoptera, which were not regularly collected, and Gerroidea, which are not subaquatic, are excluded from these tables.

Table II

	1952	1953	1954	1955	1956
Number of habitats examined (*see* Table I)	9	13	8	7	9
Number of insect species found	60	32	34	37	35
Number of non-insect species found	12	19	11	9	13
Number of insect species not previously found in the area	17	0	0	2	0
Number of insect species new to post-flood list	.	32	7	9	3

Known fauna :	1947–52	1953–56	1947–56
Number of insect species	76	51	78
Number of non-insect species	15	20	22

Table II shows that the number of species of insects found each year after the flood was much less than in 1952, while the number of non-insect species (in the groups covered by Hincks *et al.*, 1954) showed a temporary increase.

In Table III the 62 species of insects found during 1952–56 are arranged according to the highest salinity in which they were recorded; 19 species, found in 1952, which did not reappear after the flood are indicated by (X); species marked (M) were found in 1953 in water which had collected in excavations produced during the reconstruction of sea-banks: they must have migrated into the habitats during 1953.

Table IV summarises the changes in insect fauna in five habitats which were studied every year from 1952 to 1956, and all of which had relatively low salinities in 1952. It will be seen that the amount of faunal change between 1952 and

Table III.—*Maximum salinity (% sea water) in which species were found*

Group A.—Species found in 50 per cent. sea-water or more

	No. of records	%
Corixa selecta (Fieb.)	3	81
Corixa stagnalis Leach	16	81
Hydrobius fuscipes (L.)	15	81
(M) *Enochrus bicolor* (Fowler)	10	81
Ochthebius marinus (Payk.)	5	81
Ischneura elegans (v. der L.)	14	73
(M) *Agabus conspersus* (Marsh.)	23	60
(M) *Helophorus brevipalpis* Bedel	33	60
Corixa falleni (Fieb.)	4	60
Haliplus obliquus (Fabr.)	3	60
(M) *Helophorus flavipes* Fabr.	10	57

Group B.—Species found in 25–50 per cent. sea-water

	No. of records	%
Hygrotus inaequalis (Fabr.)	7	43
Hygrotus parallelogrammus (Ahr.)	6	43
(M) *Hydroporus planus* (Fabr.)	22	43
(M) *Agabus bipustulatus* (L.)	19	43
(M) *Colymbetes fuscus* (L.)	19	43
Gyrinus lateralis (Mene.)	16	40
(M) *Corixa lateralis* Leach	13	40

TABLE III—*cont.*

Group C.—Species found in 20–25 per cent. sea-water

	No. of records	%
Corixa affinis Leach	9	24
Corixa sahlbergi (Fieb.)	5	24
Corixa striata (L.)	13	24
Notonecta viridis Del.	13	24
Haliplus lineatocollis (Marsh.)	10	24
Hydroporus pubescens (Gyll.)	2	24
Ilybius fuliginosus (Fabr.)	4	24
Helophorus aquaticus (L.)	4	24
Haliplus ruficollis (Deg.)	9	24
Pyrrhosoma nymphula (Sul.)	2	24
Sympetrum striolatum (Charp.)	12	23
Plea leachi Leach	3	23
Corixa praeusta (Fieb.)	5	20
Corixa punctata (Ill.)	17	20
Notonecta glauca L.	7	20
Dytiscus circumflexus Ahr.	9	20
Hydroporus pictus (Fabr.)	3	20

Group D.—Species found only in less than 20 per cent. sea-water

	No. of records	%
Hydroporus tesselatus Drap.	4	19
Rhantus pulverosus (Steph.)	2	18
Corixa linnei (Fieb.)	3	14
Haliplus immaculatus (Ger.)	2	14
Hydroporus palustris (L.)	4	14
(X) *Ochthebius minimus* (Fabr.)	1	14
(X) *Ochthebius dilatatus* Steph.	1	14
Laccophilus minutus (L.)	1	11
Corixa panzeri (Fieb.)	5	11

Species found in 10 per cent. sea-water or less

(X) *Chloëon dipterum* (L.)
(X) *Coenagrion puellum* (L.)
(X) *Libellula quadrimaculata* L.
(X) *Aeshna cyanea* (Muell.)
(X) *Corixa nigrolineata* Fieb.
(X) *Corixa scotti* (Fieb.)
(X) *Corixa fossarum* Leach.
(X) *Corixa semistriata* (Fieb.)
(X) *Corixa venusta* (D. and S.)
(X) *Corixa limitata* (Fieb.)
(X) *Ilybius ater* (Deg.)
(X) *Haliplus apicalis* Thom.
(X) *Haliplus wehnchei* Gerh.
(X) *Hygrobia hermanni* (Fabr.)
(X) *Laccobius alutaceus* (Thom.)
(X) *Hygrotus confluens* (Fabr.)
(X) *Agabus nebulosus* (Forster)
(X) *Acilius sulcatus* (L.)

TABLE IV

	Habitat				
	LMC	BCP	IP	LBD	PMM
Salinity in 1953 (% sea-water)	73	60	43	24-27	20
Number of species of insects found in 1952 (*a*)	16	26	13	32	13
Number of these species not found in 1953 or 1954 (*b*)	15	16	7	22	5
% exterminated (100 *b*/*a*)	94	61	54	69	33
Number of species of insects found in 1953 (*c*)	2	9	12	8	20
Number of species found both in 1952 and 1953 (*d*)	0	5	4	6	9
% coincidence 1952–53 $100.2d/(a+c)$	0	28	32	30	52
Number of species which appeared in 1954, 1955 or 1956 after a gap of at least two years	19	14	8	11	13

TABLE V

	Interval			
	1952–53	1953–54	1954–55	1955–56
Number of habitats	8	7	7	7
Number of records first year (a)	124	60	63	77
Number of records second year (b)	65	63	77	85
Number of records in common (c)	30	37	46	46
% coincidence $100.2c/(a+b)$	32	60	66	57

1953 is related to the increase of salinity. Table V, which includes all habitats that were examined in two successive years, shows that the amount of change in the interval 1952–53 was about twice as great as in subsequent years.

TABLE VI

Number of species-habitat records in LMC, BCP, IP, LBD and PMM	Year				
	1952	1953	1954	1955	1956
Group A	14	25	18	16	15
Group B	16	10	14	17	19
Group C	32	13	20	22	32
Group D	33	0	5	6	7

Table VI analyses the records of insects, from the same five habitats as in Table IV, into the salinity-tolerance groups given in Table III. It shows that the species known to be euryhaline (group A) became more widespread in the summer following the flood, while groups B, C and D were adversely affected, in that order.

DISCUSSION

All the surveys were made about 15th July, and it is unlikely that the changes observed from year to year were due to seasonal differences in development. Defects in collecting can also be discounted : collecting was particularly thorough in 1953, when we had the assistance of Dr. W. D. Hincks who had had much experience of collecting in the area, but fewer species were found than in any other year. Tables IV, V and VI indicate that the observed changes in fauna are largely due to salinity changes.

Table II indicates that the fauna has become impoverished. This is shown by the reduction in the number of post-flood species to 51 (63 per cent. of the known pre-flood fauna), and by the smaller number of species found in each year. Only two species found after the flood had not been recorded before the flood (*Laccobius alutaceus* and *Rhantus pulverosus*), while some of the species which disappeared had previously been fairly common (e.g. *Chloëon dipterum*, *Corixa nigrolineata*, *Hygrobia hermanni* and *Ochthebius dilatatus*). Rice and Kelting (1955) have shown that the number of species collected from an area increases asymptotically with the number of samples, the more abundant species being recorded first and then those which are less abundant. In each annual survey, about the same amount of time was spent in collecting (about two hours at each habitat), and the sample taken each year could be regarded as of roughly constant size. The number of additional species discovered each year would, therefore, provide a rough indication of how completely the fauna is known. The additions to the known fauna in 1952 were 17 species, bringing the total to 76; however in 1956, although the post-flood faunal list had reached only 51, only three species were added. It therefore seems likely that the post-flood fauna is more fully known than the pre-flood fauna, and the estimate given above of 63 per cent. survival is probably too high.

Sampling errors become more serious in relation to the fauna of single habitats. Failure to record a species in a habitat might easily be due to its being missed in collecting, especially if it is not very common. If p is the probability of a species being recorded (a function of its frequency, conspicuousness, accessibility, *etc.*), then the chance of its being missed in n collections is $(1 - p)^n$. When p is very small, this remains high even for comparatively large values of n. For practical purposes, however, the failure to record a species for two successive years was taken as evidence of its probable absence from the habitat. Estimated on this basis, extinction of the 1952 fauna in individual habitats ranged from 33 per cent. to 94 per cent. (Table IV). Taking the five habitats of Table IV together, the percentage of extinction in 1952–53 was 63 per cent. In subsequent years it was much lower: 22 per cent. of the 1953 records were not repeated in 1954 or 1955, and 23 per cent. of the 1954 records were not repeated in 1955 or 1956.

The occurrence of a species in the same habitat in two successive years cannot, however, be taken as evidence of its survival through the intervening period, for it may have died out and become reintroduced by migration. There is evidence that the post-flood fauna is made up largely of species with good powers of migration. In 1953 ten species were found in habitats which had appeared since the flood (*Gerris thoracicus* Schumm. and the eight species marked (M) in Table III). All these species were common in the post-flood fauna generally. The common Corixidae of the post-flood fauna (*C. lateralis*, *C. stagnalis*, *C. punctata*, *C. striata*) are known to be good migrants (Brown, 1951). Taking as evidence of probable immigration the appearance of a species in a habitat from which it had not been recorded during the previous two years, 45 out of the 51 post-flood species immigrated into at least one habitat, and 29 into two or more. Of the species-habitat records of 1953, 39 per cent. represented the appearance of species in habitats where they had not been recorded since collecting started in 1947, and about one-third of the records of 1954, 1955 and 1956 indicated probable immigration. It seems reasonable to suppose, therefore, that most of the species found after the flood had re-invaded the area after their extermination.

The following species, common before the flood, were not found in 1953 but reappeared in later years: *Corixa affinis* (1954), *C. panzeri* (1956), *Gerris lacustris* (1956), *Hydroporus palustris* (1955), *Dytiscus circumflexus* (1955) and *Laccophilus minutus* (1956).

On the other hand, some species of limited distribution were found in the same habitats before and after the flood, and may have survived.

> *Plea leachi*, in PMM, 1952 and 1953, but not seen in the area since.
>
> *Notonecta glauca*, in PMM from 1952 to 1955; otherwise only in IP (1955).

Corixa falleni, in BCP, 1952 and 1953 ; otherwise only in WBB (1954).

Haliplus obliquus, in BCP, 1952 and 1953 ; otherwise only in PMM (1955).

Hydroporus pictus, in PMM before 1952, in 1953, 1954 and 1956 ; never found elsewhere.

Table III gives the highest salinity in which each species was found living, but in the case of rarer species the number of records is insufficient for reliable conclusions to be drawn. *Hydroporus tesselatus*, for example, though not recorded in a salinity above 19 per cent. sea water during 1952–56, had been found before 1952 in WBB, associated with euryhaline species. Moreover, most of the observations of high salinity were made in 1953 and 1954, and species not found in those years would necessarily be placed low in the table. Considerably more observations, on all stages of the life-cycle, need to be made, and the present data must be regarded as giving only a general picture.

Lindberg (1948) has recorded the maximum salinities in which various species occur in the Baltic Sea. The salinity of the Baltic ranges from about 55 per cent. sea water off the east coast of Denmark to fresh water at the extreme end of the Gulf of Bothnia. The Baltic insect fauna is much richer than that of Spurn, but even so there are 35 species common to the two areas, including 28 of the species in Table III. The Baltic and Spurn maximum salinities in which the following 20 species occurred differ by less than 15 per cent. sea water, ten of them (marked *) by less than 5 per cent.

*_Agabus conspersus_
*_Hydrobius fuscipes_
Helophorus brevipalpis
*_Corixa lateralis_
*_Hydroporus planus_
*_Colymbetes fuscus_
Hygrotus parallelogrammus
Agabus bipustulatus
Hygrotus inaequalis
*_Corixa sahlbergi_
*_Corixa praeusta_
Notonecta glauca
Haliplus ruficollis
Sympetrum striolatum
Corixa striata
Hydroporus pubescens
*_Corixa linnei_
*_Ilybius ater_
*_Haliplus wehnchei_
Hydroporus palustris

In the case of the remaining eight species the differences were more marked :

	Spurn (%)	Baltic (%)
Corixa stagnalis . .	81	55
Enochrus bicolor . .	81	55
Ochthebius marinus .	81	48
Haliplus obliquus .	60	34
Helophorus flavipes .	57	40
Ilybius fuliginosus .	24	48
Helophorus aquaticus .	24	48
Agabus nebulosus .	10	35

The first five species occur at Spurn in salinities which do not exist in the Baltic. The three species which were found in higher salinities in the Baltic are not common at Spurn, where their maximum salinity has possibly been underestimated.

Table III suggests that a salinity of about 25 per cent. sea water is critical to many fresh water insects. No Ephemeroptera or Trichoptera were found above this salinity, which was also fatal to most Odonata. Hemiptera, Haliplidae, Hydrophilidae and Dytiscidae. A few species of each of these last groups were able to survive at higher salinities, where the Coleoptera were relatively more abundant. Salinities from 65 per cent. to 85 per cent. sea water were colonised almost exclusively by *Corixa stagnalis*, Hydrophilid beetles and Diptera. Insects have colonised almost every type of fresh water and terrestrial habitat ; the euryhaline habit represents several independent trends towards the production of marine species. A study of the anatomy and physiology of these euryhaline species might explain why so few species of insects live in sea water, but apart from the work of Claus (1937) on adults of *Corixa stagnalis* and of Wigglesworth (1938) on *Aëdes*, this problem has received little attention.

Before the flood, the euryhaline species of groups A and B were characteristic of the more saline habitats. They were, however, by no means confined to these habitats : in 1952 species of these groups were found in all the habitats of low salinity. With the rise of salinity of the formerly comparatively freshwater habitats in 1953, group A increased in importance, group B diminished slightly, group C was considerably reduced and group D disappeared. Group B had recovered in 1955, and group C in 1956, but group D was still very adversely affected in 1956. As groups B and C increased during recovery from the flood, group A diminished. The temporary increase of group A in 1953 might be due to (*a*) their preference for water of high salinity, (*b*) the absence of competition from less euryhaline species, or (*c*) their greater ability to migrate into the area. In 1953 species of groups C and D were found only in PMM, LBD and BD (east), and there was only one record of each of the 13 species found. In 1954 they had spread to IP, PP and WBB, and in 1955 to LMC. The species thus tended to become more widely distributed as the salinity of the habitats declined. Although the salinities did not decline further in 1956, the species continued to extend their range : the average number of habitats in which each species of group C was found (*i.e.* number of species-habitat records ÷ number of species found) rose from 1·0 in 1953 to 1·8 in 1955, and rose again to 2·8 in 1956. Repopulation of available habitats thus showed a lag, owing perhaps to the limited powers of migration of some species of the group. Perhaps for the same reason, most of the species of group D had not returned by 1956, even though the salinity of most of the habitats had been restored to its preflood level. The absence of some stenohaline species known to be ready migrants, such as *Corixa nigrolineata*, cannot however be explained in this way.

The floods of 1953 are in no way unique. Spurn has been flooded in a similar way on many previous occasions, on each of which stenohaline species would be eliminated from the area, and a group of euryhaline species, with good powers of migration, would become temporarily dominant. As the stenohaline species return, the euryhaline species would remain as a dominant element of the fauna only in the more brackish habitats.

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SOME OBSERVATIONS ON THE RESPIRATION OF YOUNG NYMPHS OF *SCHISTOCERCA GREGARIA* (FORSKÅL) IN RELATION TO PHASE AND REARING DENSITY

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Introduction

This investigation was undertaken to compare the respiratory rates of locusts of the gregarious phase and the solitary phase, and to study the effect of the phase of a parent locust on the respiratory rate of its progeny.

Acknowledgments

My thanks are due to Dr. N. Waloff for suggesting this problem, to the Anti-Locust Research Centre for the supply of locusts, and to Mr. D. E. Davies of that Centre for advice on the statistical treatment.

Materials and Methods

The work was carried out with hoppers (nymphs) of the first and second instars of the Desert Locust, *Schistocerca gregaria* (Forsk.). Two forms of hatchlings were used, the black gregarious form produced from parents reared for many generations in the laboratory under crowded conditions and designated throughout this paper by the symbol *G*, and the green solitary form from parents reared in isolation for at least one generation and designated by the symbol *S*.

Both forms were kept in a constant temperature room maintained at 29° C. and 70 per cent. relative humidity. In many cases, successive batches of eggs from the same female were used, so that the batches of hoppers were as homogeneous as possible. The hatchlings from each egg-pod were divided into two batches 1–3 hours after hatching, half being kept under crowded conditions and the others singly. All were kept in 1-pound jam jars with muslin tops, the crowded conditions being obtained by enclosing 20 in the same jar, and isolation by putting only one in each jar. The hoppers were fed on grass, which was changed daily ; equal amounts were used in all experiments. A sheet of white paper was pasted round each jar to give uniform background. Under these conditions the first instar was relatively short, moulting occurring during the fifth day. Respiration measurements were made on first-instar hoppers when they were three days old and second-instar hoppers when they were seven days old ; in both cases, two days elapsed between the taking of measurements and the time of moulting. This was essential since at the time of moulting respiration was considerably altered.

The respiratory exchange was measured by means of a Warburg constant-volume respirometer. The flasks used were specially adapted, as it was found difficult to keep the hoppers out of the KOH except by maintaining them in the side arms of the flasks. This was done by carefully cementing a circular piece of gauze (the same size and weight in each case) over the opening of the side arm of each flask (fig. 1). A single hopper was placed in the side arm, and the flask connected to the manometer. After an hour, readings were taken every 15 minutes over a period of three hours. Figure 2 is a graph showing the regular manner of oxygen uptake by the various groups of hoppers during the experimental period. The hoppers used were weighed before and after the experiments, the mean weight being taken in each case. In each experiment with a given batch of hoppers (either *G* or *S*), half of the flasks received hoppers reared gregariously and half received hoppers reared solitarily. In practice, five of each kind were used in each experiment, either five *GG* and five *GS*, or five *SS* and five *SG*, the first letter indicating the phase of the parents and the second indicating whether the hoppers were reared crowded or singly. All the results were corrected for temperature and pressure.

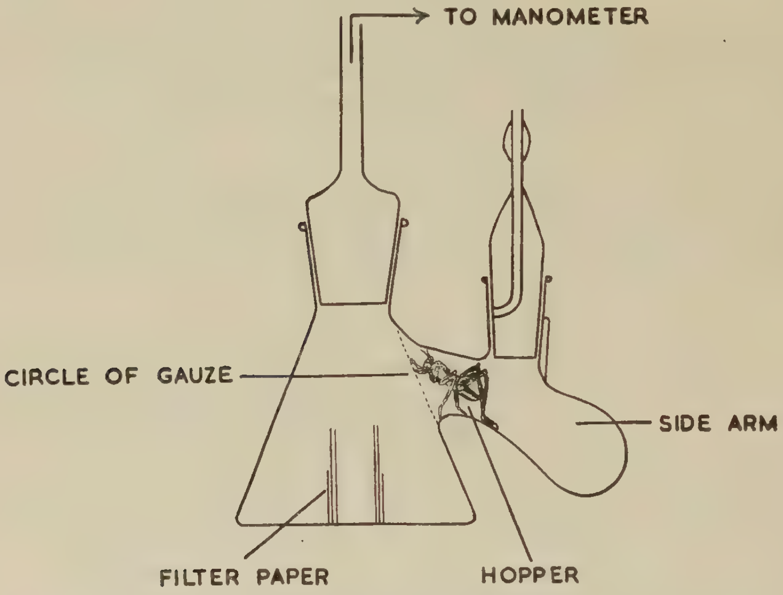

Fig. 1.—Flask with hopper in side arm.

The respiration measurements were carried out at the temperature at which the hoppers were reared, *i.e.* 29° C. Before each experiment, the hoppers were weighed and isolated in tubes (maintained at 29° C.) for two hours; this was to ensure that there was in the gregariously reared hoppers, no additional activity, due to visual and tactile stimuli, as could occur if they were tested immediately after withdrawal from a crowded jar. At this temperature, the hoppers were initially quite active, but they soon settled down in the confined space of the side arm under subdued diffuse lighting, and rested on the small piece of gauze throughout the experiment. Activity measurements, which involved the recording of a standard set of movements, including antennal flexure, cleaning reflexes and posture, confirmed that there was no significant difference in the level of activity in the four types.

With the hoppers from gregarious parents (*G*), 40 observations were made, 20 on hoppers kept in crowds (*GG*) and 20 on hoppers kept solitarily (*GS*). With the hoppers from isolated parents (*S*), only 20 observations were made, ten on *SG* and ten on *SS*.

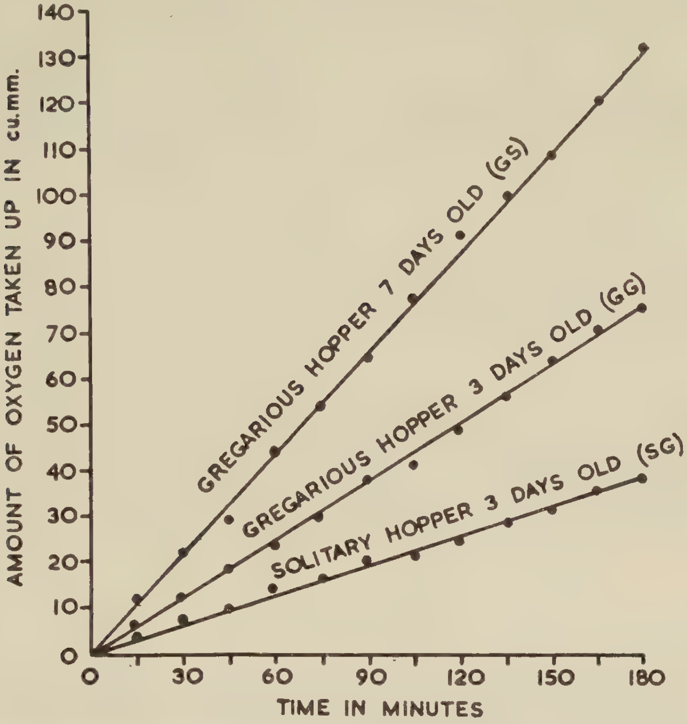

FIG. 2.—Graphs showing constancy of oxygen uptake within the three-hour period. (The three graphs are not comparable since they represent oxygen uptake of whole insects, weights having been disregarded.)

RESULTS

The results are given in Table I, in which the data are condensed to show only the amount of oxygen taken up per insect, expressed in c. mm./mg. of body weight/15 minutes.

From an analysis of variance of the data of Table I for first-instar hoppers, there is a strong indication that the group means (*GG*, *GS*, *SS*, *SG*) are different. It suggests that the effect of parentage on the mean oxygen uptake is highly significant ($P < 0{\cdot}001$). It also shows that the rearing is non-significantly different in its effect on the mean oxygen uptake ($P > 0{\cdot}2$), although there is a significant measure of interaction of parentage and rearing ($P < 0{\cdot}05$). Further analysis was carried out on the effects of rearing and parentage combined, the Tukey Gap method (Tukey, 1949) being employed (Table II). The group means, when ranked and tested, clearly indicate that interaction is taking place between parentage and rearing. This is shown by the fact that the

TABLE I.—*Oxygen uptake of first- and second-instar hoppers of* Schistocerca gregaria *at* 29° *C.*

Each number represents the amount of oxygen taken up by a single hopper in c.mm./mg./15 minutes.

Exp.										
	First-instar hoppers, black, three days old ; gregarious parents									
	1/*GS*	2/*GS*	3/*GS*	4/*GS*	5/*GS*	6/*GG*	7/*GG*	8/*GG*	9/*GG*	10/*GG*
1 .	0·2299	0·2271	0·1627	0·2658	0·2189	0·2733	0·1879	0·2966	0·2220	0·1951
2 .	0·1752	0·2260	0·1794	0·2414	0·1957	0·2152	0·2085	0·2036	0·2061	0·1925
3 .	0·2613	0·2638	0·2891	0·2794	0·2753	0·2094	0·2050	0·1986	0·2076	0·2648
4 .	0·2183	0·2243	0·2030	0·1933	0·2445	0·2219	0·2252	0·2545	0·1999	0·2300
	First-instar hoppers, green, three days old ; solitary parents									
	1/*SS*	2/*SS*	3/*SS*	4/*SS*	5/*SS*	6/*SG*	7/*SG*	8/*SG*	9/*SG*	10/*SG*
5 .	0·1672	0·1888	0·1193	0·1181	0·1390	0·1685	0·1685	0·1697	0·2049	0·1995
6 .	0·1621	0·1394	0·1346	0·1256	0·1520	0·1599	0·1601	0·1809	0·1571	0·1638
	Second-instar hoppers, black, and green, seven days old ; gregarious parents									
	1/*GS*	2/*GS*	3/*GS*	4/*GS*	5/*GS*	6/*GG*	7/*GG*	8/*GG*	9/*GG*	10/*GG*
7 .	0·2135	0·2787	0·2372	0·1935	0·1901	0·2132	0·2528	0·2497	0·2431	0·2812
8 .	0·1912	0·1929	0·1981	0·2105	0·2591	0·1968	0·2006	0·2651	0·2548	0·2259
9 .	0·1839	0·2049	0·1888	0·2075	0·2261	0·2422	0·2444	0·2947	0·2998	0·2369
10 .	0·1944	0·2112	0·2144	0·1816	0·2206	0·2829	0·3184	0·3157	0·2773	0·2793

First letter indicates phase status of parent.
Second letter indicates method of rearing.

differences produced by the rearing procedures used for hoppers of solitary parents is significant, whilst those from gregarious parents are opposite and non-significant. Also, the gap between the *largest* solitary uptake (in *SG*) and the *smallest* gregarious uptake (in *GG*) is significant, which separates hoppers from solitary parents and gregarious parents, respectively. To summarise these results, it can be said that the oxygen uptake of the black hoppers from gregarious parents is considerably higher than that of the green hoppers from solitary parents, irrespective of rearing procedures ; there is no significant difference in the oxygen uptake of the hoppers from gregarious parents at three days old, whether reared solitarily or gregariously, but the hoppers from solitary parents reared gregariously from hatching showed a significantly higher oxygen uptake after three days than those reared solitarily for the same period.

TABLE II.—*Analysis relating to the interaction of parentage and rearing on oxygen uptake of first-instar hoppers of the Desert Locust*

Group means ranked in order of magnitude		Observed gap	
G.S. .	0·22872	.	.
G.G. .	0·220885	0·007835	<20% gap (0·0141963), non-significant.
S.G. .	0·173290	0·047595	> 1% gap (0·0291378), highly significant.
S.S. .	0·144610	0·028680	> 2% gap (0·0261802), 1% gap (0·0291378), highly significant.

The same experimental procedure was used for testing second-instar hoppers seven days old. Unfortunately, green hoppers from solitary parents were not available in this instar.

Of the black hoppers from gregarious parents, 85 per cent. of those reared in isolation changed to green, coming to resemble the green hoppers from solitary parents more closely. Applying the method of comparison of two means to the data in Table I relating to second-instar hoppers :

Mean uptake of oxygen/mg./15 minutes for $GG = 0{\cdot}2589$ c.mm.
Mean uptake of oxygen/mg./15 minutes for $GS = 0{\cdot}2099$ c.mm.
$t = 5{\cdot}07$ (correct to three significant figures)
Degrees of freedom = 38
$\therefore P < 0{\cdot}001$ (highly significant).

When the hoppers were seven days old, the manner of rearing affected significantly the amount of oxygen consumed by hoppers of gregarious parentage, those reared gregariously having a much higher oxygen consumption than those reared solitarily. This is of considerable interest since at three days old the effect was not apparent.

The hoppers were weighed on hatching and when used in experiments three days later. In each experiment the weights of 30 hoppers (from the same egg pod) were taken ; 15 were subsequently reared solitarily and the others gregariously. As there were two types of parents, this amounted to 60 hoppers in all (Group 1). The experiments were repeated two days later (Group 2) and the initial results plus those of the replicates treated together in the subsequent analysis.

Applying the *F* test :

$$\left.\begin{array}{lr} \text{Error mean square} \quad . \quad . & 4{\cdot}143 \\ \text{Percentage mean square} \quad . & 1333{\cdot}333 \end{array}\right\} \left.\begin{array}{lr} F = & 321{\cdot}833 \\ d.f. = & 1{\cdot}118 \end{array}\right\} P < 0{\cdot}1 \text{ per cent.}$$

Thus the initial weights of hoppers from gregarious parents were significantly greater than those from solitary parents. A covariance analysis was carried out, and the information extracted from this analysis can be summarised as follows :

(1) When the expected effect of correlation of initial weight with final weight was removed, the greatest gain in weight was obtained with hoppers from gregarious parents, reared gregariously, while the least gain was obtained by hoppers from solitary parents, reared solitarily.

(2) Gregariously reared hoppers of solitary parentage gained significantly more than solitarily reared hoppers from gregarious parents.

(3) The parental rearing interaction was non-significant, contrasting with the previous analysis.

The experiments would have been more satisfactory had both the initial experiments and the replicates been carried out on the same day. There appears to have been some difference, associated with different dates, in the stocks used.

DISCUSSION

In all cases of measurement of gas exchange, the results must be converted to a form in which they are easily comparable. If gaseous exchange is expressed in c.mm./15 minutes/whole insect, differences in size and weight will not be taken into account, and a direct comparison will be inaccurate. The only two possible methods of comparison are either c.mm./15 minutes/unit of surface area, or c. mm.15 minutes/unit weight.

Surfaces of living insects are not constant, nor are they easily measured, and since the hoppers used were only first and second instar with not very large weight differences, the second form of expressing gas exchange was thought to be the more suitable, *viz.* c.mm./15 minutes/unit weight. Zeuthen (1947) has made a detailed review of the literature on the relation between body size and metabolic rate and has found that, among insects in general, the metabolic rate per unit weight decreases with increasing size. Yet Edwards (1946) found in *Talorchestia*, *Musca* and *Melanotus*, that respiration was nearly proportional to weight. In the present case, a series of readings was taken and weight plotted against oxygen uptake/15 minutes, and over the small range of weights used, a direct linear relationship existed (fig. 3). The method of expression c.mm. 15 minutes/mg. is accurate over the range of weights encountered, and gives a straightforward method of comparison in all cases.

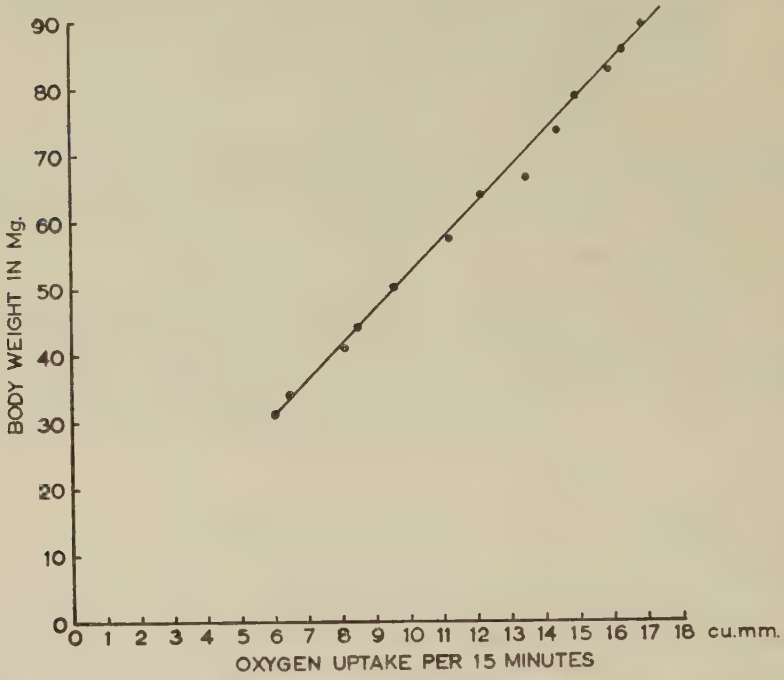

FIG. 3.—Graph showing linear relationship between oxygen uptake and body weight of hoppers (*GS*).

Previous work on locust respiration includes that of Chauvin (1941). He carried out experiments on respiratory movements in *Schistocerca* by attaching a needle to the abdomen and recording the movements on a smoked drum. He measured in this way abdominal movements of fifth-instar hoppers of both gregarious and solitary forms. In the case of the gregarious hoppers, he recorded a trace showing a series of small movements followed by periodic larger ones, while with the solitary hoppers of the same instar, the trace was of the same nature but the amplitude of the smaller movements was much less whilst the larger periodic ones were nearly the same. From this type of experimental work, Chauvin concludes that metabolism of gregarious hoppers is higher than that of solitary hoppers of similar age. Butler and Innes (1936), working with *Locusta migratoria* adults, have shown that the oxygen consumption of the phase *solitaria* is significantly lower than that of the phase *gregaria.* The present data confirm these conclusions.

The most obvious difference between solitary and gregarious hoppers is in their colour, but, according to Uvarov (1948), the gregarious hoppers are on the whole more active. Volkonsky (1939) noted that the increased activity of the gregarious hoppers led to a rise in temperature over that of the solitary hoppers. Again, because of their black pigmentation, the gregarious hoppers when exposed to sunlight acquire a higher body temperature than do the green solitary forms (Strel'nikov, 1936) and since changes in temperature are intimately connected with metabolic rates, this may partly explain the differences in respiratory rates of the gregarious and solitary forms.

SUMMARY

1. A comparison was made of respiratory rates in first- and second-instar hoppers of *Schistocerca* reared gregariously and solitarily.

2. Three-day-old hoppers from gregarious parents have a higher respiratory rate than those from solitary parents.

3. The density of rearing during the first three days had no significant effect on the respiratory rate of hoppers of gregarious parentage, but had a pronounced effect on that of hoppers of solitary parentage. The changes in respiration due to differences in rearing became evident in hoppers of gregarious parentage after seven days.

4. The initial weight of hoppers from gregarious parents was significantly greater than that of hoppers from solitary parents. The greatest gain in weight (after three days) was obtained with hoppers from gregarious parents reared gregariously, whilst the least gain was recorded in hoppers from solitary parents reared solitarily. Gregariously reared hoppers of solitary parentage gained significantly more than solitarily reared hoppers from gregarious parents.

5. A direct linear relationship was found between oxygen uptake and body weight.

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SOME OBSERVATIONS ON THE NATURAL HISTORY OF *ACANTHASPIS PETAX* STÅL (HEMIPTERA: REDUVIIDAE) LIVING IN TERMITE MOUNDS IN UGANDA

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Insects of the genus *Acanthaspis* Amyot and Serville, together with two other Reduviid genera, *Reduvius* Lamarck and *Paredocla* Jeannel, are known to disguise themselves with accumulations of debris stuck on to their bodies (Miller, 1956). It has been suggested that " the disguise is an aid in the capture of prey and also that it is protective against enemies " (Miller, *op. cit.* : 98), but this has not been substantiated in the past. Odhiambo (1958) recently reported laboratory observations with *Acanthaspis petax* Stål which lend some support to those suggestions.

The present paper records observations carried out with populations of *A. petax* in their natural habitat, which give some further support to the suggestions outlined above. Other observations are recorded which show how this insect is able to occupy its peculiar habitat, deserted termitaria.

Habitat

A. petax is widely distributed in Uganda and usually occupies termite mounds which have been abandoned by their builders. These bugs may also be found living in the cracks of mud walls of huts. The observations recorded here were made at Serere Agricultural Experiment Station in the Kioga Basin of the Short Grass Zone (as described by Hansford, 1940; and Thomas, 1940). This area is studded with numerous large mounds built by the fungus-growing termites—particularly *Macrotermes* spp. On abandoned termitaria, small and large tunnels (diameter ½–10 inches) in the outer crust very often become exposed as a result of weathering action. The latter is also responsible for numerous small depressions and cracks on the mound surface. It is in these tunnels, cracks and depressions that the bugs occur. It also appears that it is only the mounds of fungus-growing termites that are so inhabited. On a large mound (4–5 feet high) inhabited by these bugs over 50 nymphs and ten adults or more may be found, whereas on small mounds (hardly above ground-level) not more than four to five nymphs may occur.

In one case a third instar nymph was found on a large mound that had been extensively damaged by land clearing operations and contained only a small inactive termite colony; in another case, a previously abandoned termitarium was gradually recolonised by termites, and after 5–6 weeks only one *Acanthaspis* nymph (fifth instar) remained, where earlier 20 or more were regularly seen. It is probable, therefore, that *Acanthaspis* only live in abandoned termitaria. Moreover, termitaria that are shaded from the sun for the greater part of the day are preferred to the more exposed mounds.

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THE PROTECTIVE COVERING

One of the most interesting things about *A. petax* is its habit of camouflage. Two main types of protective covering are found on the nymphs:

(1) Sand particles which are stuck on to the entire body with the exception of the second to fourth segments of the antennae, the *fossula spongiosa* (on the fore and median tibiae), venter of the head, and the narrow prothoracic sternum. The soil particles, being taken from the mound, afford an excellent camouflage.

(2) The " camouflage of corpses ". This consists predominantly of corpses of small insects, but plant parts are often included—bits of leaves, seed coats, grass stems, *etc.* Among the insect corpses, ants are the most numerous; but flies, small grasshoppers, beetles, and even cast skins of previous moultings may be included. All these are interlaced with silk-like threads and attached to the dorsum of the abdomen by a similar secretion exuded by secretory hairs.

The composition of the camouflage of corpses is always changing, as, after the completion of feeding, the nymphs almost invariably add the corpses of their prey to the " coat ".

The adults do not have such a covering, as stated by Miller (*op. cit.*). Moreover, adults are conspicuously coloured, with a red and black pattern; and since they are nocturnal in habit (*see below*) camouflage would seem superfluous.

DAILY PATTERN OF ACTIVITY

Nymphs

Nymphs of *A. petax* usually appear inactive. This is because their initial reaction to any movement is either to flatten themselves to the substratum, in which case they are extremely difficult to spot, or to disappear into tunnels, from which they may not emerge for half-an-hour or more.

Sustained observation shows that the nymphs exhibit a complex pattern of activity. In order to investigate this, the population of nymphs inhabiting a large termitarium (5 feet high) was selected for detailed study. On two days, 24 and 25 August, 1957, counts were made hourly from 6 a.m. to 8 p.m. (East African Standard Time). A note was made of the number of nymphs visible inside the tunnels (and within $\frac{1}{2}$ inch of the tunnel entrance) separately from those outside.

It will be seen (fig. 1) that the greatest activity of the nymphal population (as measured by the relative numbers of nymphs on the mound and within entrances to tunnels) is between 10 a.m. and 5 p.m. In the evening, the majority enter the tunnels for the night, and by 8 p.m. nymphal activity on the mounds ceases until the next morning. A small proportion usually spend the night on the mound surface. This is especially the case with first and second instar nymphs, most of which take refuge in the numerous small cracks and depressions. There

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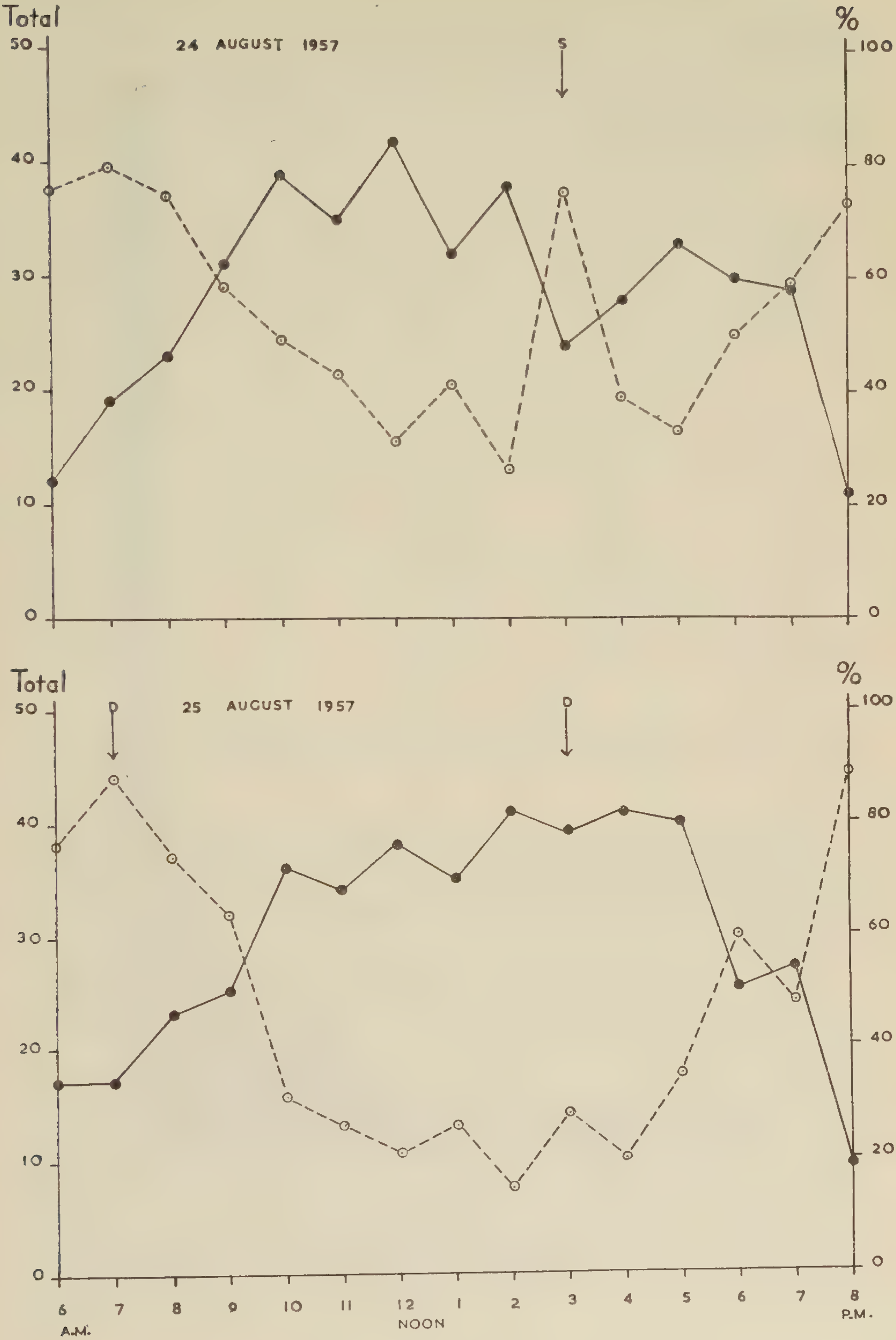
FIG. 1.—Numbers of nymphs counted on a large termite mound for a 14-hour period for two consecutive days. Continuous line (●———●), total number of nymphs. Broken line (○– – – –○), per cent. number of nymphs within entrances to tunnels. (↓ indicates rain (*S*, showers, *D*, drizzle)). East African Standard Time.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is a little movement just before first light (6 a.m.), but it is not until after this time that there is any pronounced activity. Less detailed observations made two weeks previously revealed a similar pattern of behaviour.

Four fourth instar nymphs on a termitarium were observed for an hour each during one afternoon and the details of their activity recorded for every 5 minute interval (Table I).

TABLE I.—*Time (in seconds) spent by individual fourth instar nymphs in locomotion on a termite mound during the afternoon of 25th August*, 1957

Interval (5 min.)	Nymph I 12.12–1.12 p.m.	Nymph II 1.18–2.18 p.m.	Nymph III 3.10–4.10 p.m.	Nymph IV 4.15–5.15 p.m.
1	90 *H*	67 *H*	109	103
2	118 *H*	13 *HC*	5	56
3	107	5	55	14
4	19	78	5	2
5	12 *H*	20 *HC*	13	12
6	2	22	0	42 *H*
7	66 *HC*	11 *HC*	0	76
8	74	0	0	1
9	0	5	10 *P*	46
10	1	36	0	61
11	10 *H*	60 *P*	0	89
12	43 *P*	16 *P*	0	66
Total	542	333	197	568
Per cent. time spent in movement	15·0	9·2	5·5	15·8

HC, nymph pursuing and catching an insect; *H*, nymph pursuing prey; *P*, nymph preening.

It is clear that even during the time of peak activity (that is, during mid-morning to late afternoon) only about 10 per cent. of the time is spent in walking. It is interesting to note that nymphs II and III spent significantly less time in walking than I and IV; this is possibly because the former were well fed and hence became less active.

As noted earlier (Odhiambo, 1958), the nymphs progress by making rapid movements of short duration. This is clearly brought out by figure 2, in which the movements made by the four nymphs recorded in Table I were classified according to the time taken by them.

Nearly 55 per cent. of the movements, it will be seen, took 1–5 seconds to accomplish, and, from my records, about 43 per cent. (*i.e.* 72 of the 169 movements recorded) took only 1–3 seconds. We may conclude, therefore, that locomotory movements made by nymphs are characteristically of short duration, of about 1–5 seconds, and sustained movements of more than 30 seconds are uncommon. This type of movement, which enhances the effectiveness of the camouflage and makes it more difficult to locate *Acanthaspis* nymphs, is also carried over to the adult stage. Sustained movements are usually employed when escaping from danger or when in pursuit of prey. When stalking

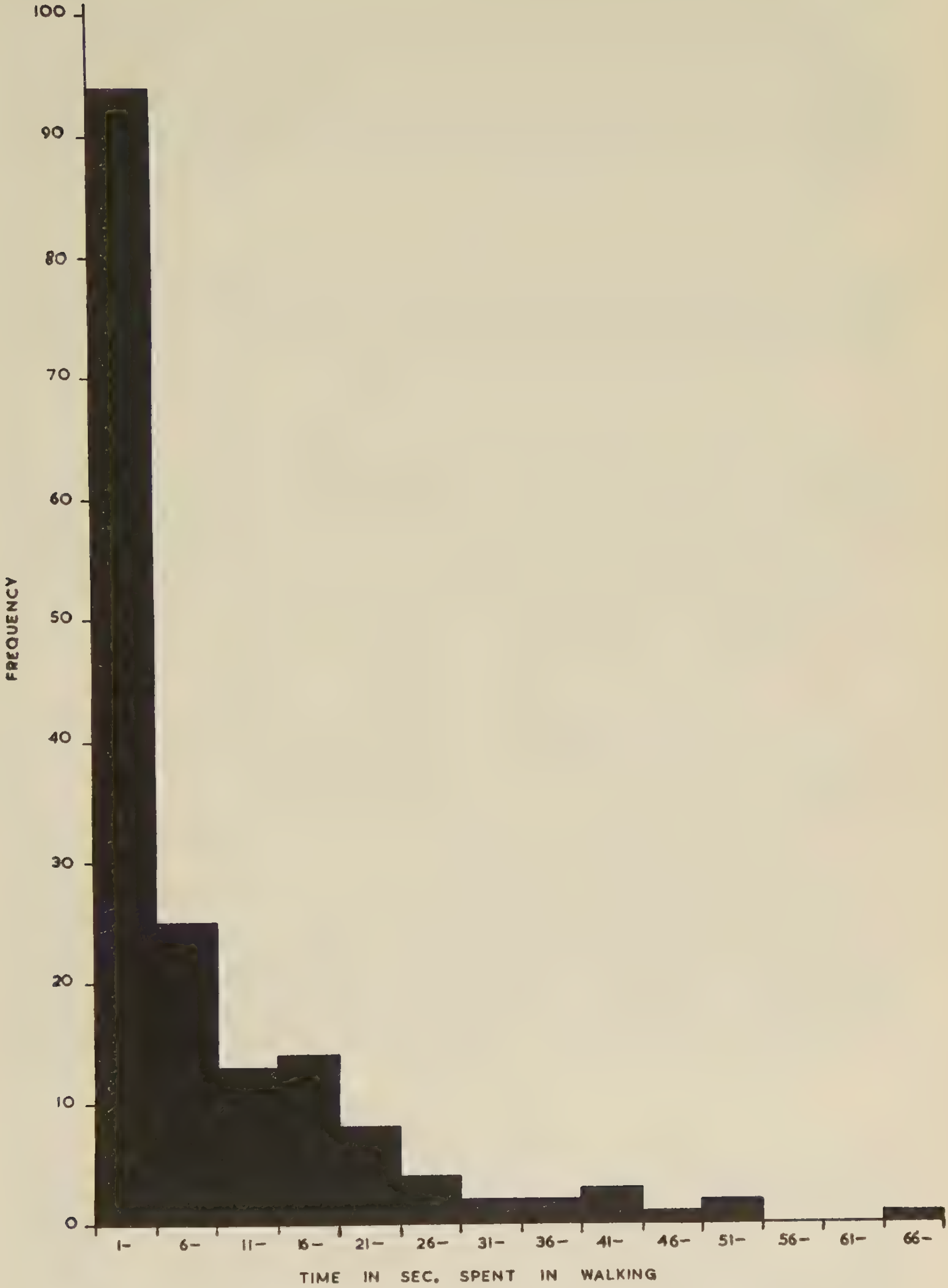

FIG. 2.—Duration of walking periods of four nymphs (fourth instar) during early afternoon, each individual observed for an hour. *Frequency* stands for number of times that movement of a particular time category is recorded.

prey, or when walking generally over the mound, on the other hand, movements of short duration abruptly punctuated by long intervals are usual.

An activity best described by the term " preening " takes a large part of the time of the nymphs. They clean their long and delicate antennae by repeatedly passing them between the *fossula spongiosa* of the anterior tibiae. At the same time the nymph usually adjusts its camouflage of corpses by using its hind legs, and may also add new material to it.

Adults

Adults are largely nocturnal. They start emerging from their tunnels at about 5 p.m. and reach maximum activity after about 8 p.m., returning again to their burrows at 6 a.m. Though adults are seen occasionally during the day, they remain within entrances to the tunnels.

Movement Between Tunnels

Several nymphs were marked by removing their original camouflage of corpses and offering some other conspicuous material (*e.g.* small feathers) to use for their " coat ". It was possible to follow the movements of such marked nymphs for two days before they lost their identity by adding the more usual materials. From such observations it was found that a nymph had no one particular tunnel or crack or depression which it habitually occupied, but that it took refuge in the nearest one.

FEEDING HABITS

Villiers (1948, quoting Jeannel, 1919) suggests that *Acanthaspis* feeds on ants. Though Odhiambo (1958) has fed ants and termites to *A. petax* in the laboratory, this evidence alone does not establish the fact that the bugs do indeed feed on ants and termites in their natural habitat.

Nymphs have been observed on numerous occasions feeding on small ants that usually visit termitaria, especially in the early morning and towards evening. Flying ants frequently congregate on top of large mounds during their mating flights, and these are also captured. On a few occasions nymphs have been seen feeding on termites. Corpses of other insects (flies, small grasshoppers and beetles) incorporated in the camouflage coat presumably represent previous prey. Various other insects and arthropods visit termitaria, and all these are potential prey for *Acanthaspis* nymphs. Crickets sometimes occupy tunnels in company with these nymphs, and the latter do not appear to molest them.

Pursuit of Prey

Prey is caught in the way previously described (Odhiambo, 1958). When a potential victim moves within 6 inches of a nymph, the latter immediately begins to stalk it, employing its characteristic short-and-abrupt movements, continuing until facing the side of the intended prey. When it comes within striking distance, it suddenly springs on the prey, impaling it on its proboscis. If it misses or if the prey escapes before the nymph comes within striking distance, the latter usually gives chase, abandoning its short-and-abrupt type of movement. From many pursuits observed, less than half have been successful.

Ants are not the only prey hunted, though they undoubtedly form the main diet of *Acanthaspis* nymphs. A tachinid, an Ichneumon fly, *Geocoris* bugs (Lygaeidae), and even a spider, have also been observed being pursued by nymphs, though in all cases the intended prey escaped capture. When ants are few on termite mounds, especially during mid-day, *Acanthaspis* nymphs frequently go down to ground level or climb trees and shrubs near the mound to forage for insects. It is at this time that the nymphs are most active in hunting. At 6–7 a.m. they appear not to attempt the capture of ants which come near them.

Frequency of Feeding

A number of nymphs were caught from several mounds, their camouflage of corpses removed, and the abdomen of each examined to determine whether it was "distended", "full" or "empty", thus giving some indication of its having fed recently or not (Table II). A full abdomen usually took about 3–4 days before it became empty, a distended one 5–7 days.

TABLE II.—*Frequency of fed nymphs collected from several termite mounds at Serere, Uganda*

Nymphal instar	Mean length of body (mm.)	Range of mean length (mm.)	State of abdomen: Distended or full	State of abdomen: Empty	Total
1	2·5	2·0–3·0	2	3	5
2	3·5	3·0–4·5	0	6	6
3	5·2	4·0–6·5	10	13	23
4	7·7	6·0–9·5	15	23	38
5	11·5	9·5–14·0	23	13	36
Total	—	—	50	58	108

Out of a total of 108 nymphs more than 50 per cent. had empty abdomens. Thus a high proportion of the nymphal population had not had a meal, or at any rate not a substantial one, for at least 3–4 days.

Nymphs with full or distended abdomens kept in isolation have remained alive for 12 or more days without food or water. They resumed feeding when offered ants or termites and appeared to be quite normal in their general behaviour.

ESCAPE FROM ENEMIES

Apart from the camouflaging habits which may enable them to escape detection, *Acanthaspis* nymphs have also other patterns of behaviour which help them to escape from their enemies.

When an "enemy" approaches a nymph, the latter usually stops all movements and activities abruptly (as noted above). If the intruder continues to move towards the nymph, the latter quickly runs to the nearest tunnel. If this is more than about 6–9 inches away, the nymph runs in short spurts, stopping inside cracks and depressions, on the way. If, however, the intruder is still hot in pursuit at the time the nymph reaches the entrance, the nymph voluntarily drops into, instead of running down, the tunnel.

If the nymph is caught, it feigns death, and even if it is then immediately released it does not show any sign of movement for several minutes. As a rule, however, it is very difficult to catch a nymph, for when one attempts to do so all that is usually found in the hand is the camouflage of corpses ; the nymph itself remains flattened on to the substratum, and is then extremely difficult to detect.

Odhiambo (1958) has already described how the camouflage of corpses may be used to protect nymphs from the attack of large ants. Many authors have suggested the probable use of stink glands as a defence device, but no attempt has so far been made to investigate this in the case of *A. petax*.

Discussion

Hesse (1955) has found that in the termitaria built by the large mound-builders in East Africa—*Macrotermes*, *Odontotermes* and *Pseudacanthotermes*—the humidity of the interior of a termite-inhabited mound is kept at a much higher level than the environs, the water having been produced metabolically by the termites. In the case of deserted mounds, however, he states that the humidity is lower and it is in equilibrium with that of the surrounding area. It does not appear, therefore, that *Acanthaspis* is selecting a high humidity habitat when it lives in deserted mounds.

Deserted termitaria possess many tunnels and numerous cracks and depressions, and mud walls have many cracks ; it would be expected that various insects and arthropods would investigate them as possible refuges. It would seem, therefore, that in occupying this habitat *A. petax* has selected a place which is peculiarly suitable as a hunting ground and as a refuge for the night and from enemies. It is possible that moulting also takes place within the tunnels. When there were showers of rain a large number of nymphs went inside the tunnels (fig. 1), indicating that they may be used as a refuge from unfavourable weather.

The camouflaging habits of the nymphs, added to their peculiar way of walking and their escape mechanism, make them well adapted to their seemingly unattractive habitat. The fact that the nymphs can go without food or water for a relatively long time only adds to their effectiveness in occupying this particular ecological niche.

Acknowledgments

The writer wishes to record his indebtedness to Mr. J. Bowden for a critical reading of this paper ; he is also grateful to Mr. W. R. Ingram, Mr. J. C. Davies and Mr. P. E. S. Whalley for many suggestions.

Summary

Acanthaspis petax Stål lives in deserted termite mounds and sometimes in cracks in mud walls in Uganda. The nymphs have a protective covering consisting of sand particles adhering to the body, and a " coat " consisting of corpses of insect prey, cast skins of previous moultings and vegetable matter.

These, added to their characteristic sudden and rapid movements, effectively camouflage the nymphs from their enemies and prey alike.

An account of the pattern of daily activity is given. Nymphs are diurnal while adults are nocturnal. Nymphs were observed to feed on ants and termites ; they can remain several days without feeding.

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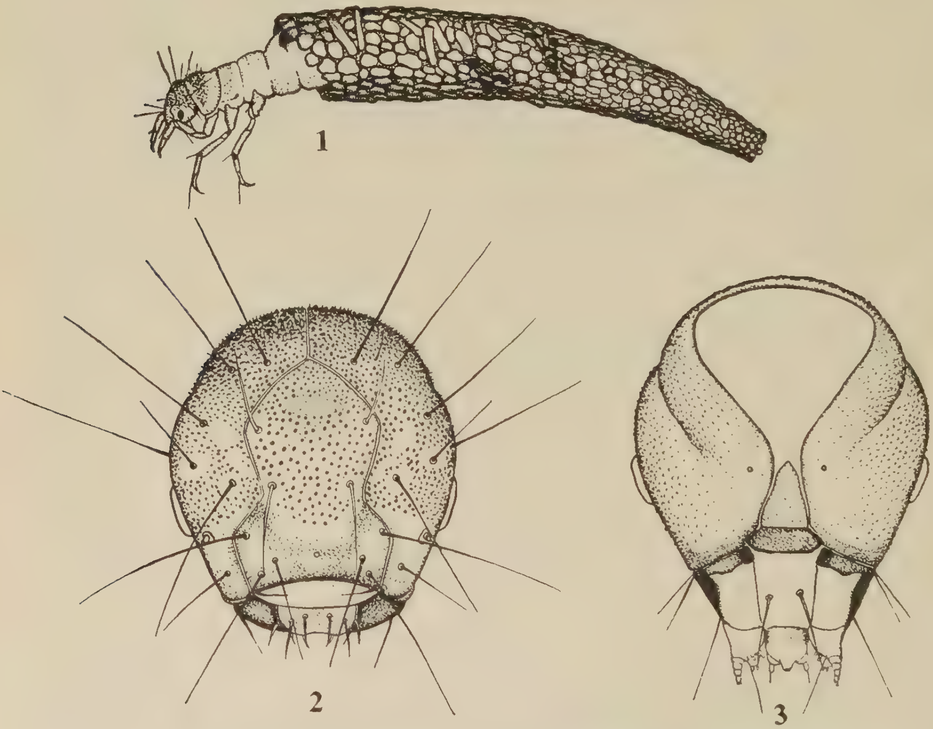
LARVAE OF THE BRITISH TRICHOPTERA: 52

By N. E. Hickin

Enoicyla pusilla Burmeister (Limnephilidae)

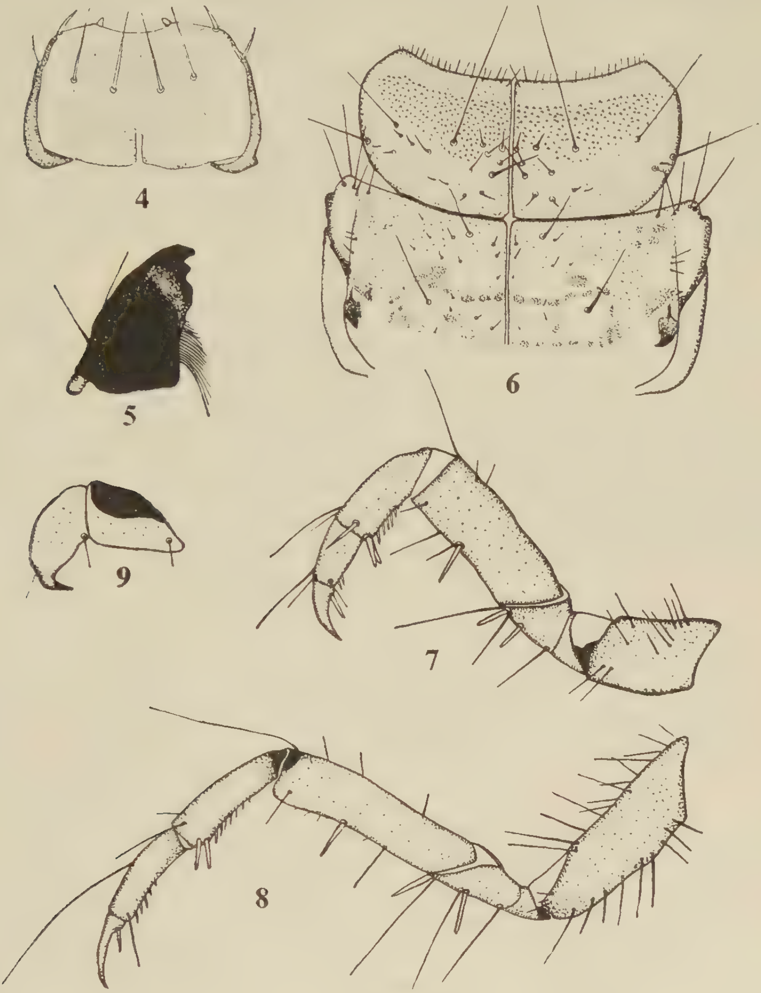
Enoicyla pusilla Burmeister was collected a number of times between 1868 and 1879 by McLachlan and Fletcher in localities near the City of Worcester. Since then it has not been recorded from the British Isles until, on 22nd April, 1957 my daughter Sari and I collected several larvae from a small meadow on the Worcestershire edge of Wyre Forest. The first larvae were found in a tent which my daughter had pitched in the meadow, but subsequently they were found in large numbers at the bases of tufts of grass within 10 feet of the hedge, or forest edge, usually under dead oak leaves which surrounded each grass tuft and often within mouse tunnels. When the particular habitat had been recognised the larvae were found very easily—about 200 being observed within an hour.



Figs. 1–3.—*Enoicyla pusilla* Burmeister. (1) Larva in case. (2) Head from the front. (3) Head from behind.

PROC. R. ENT. SOC. LOND. (A) 33. PTS. 10–12. (DEC. 1958).

Enoicyla pusilla is unique among the British Trichoptera in possessing terrestrial larvae and pupae, and in the adult female being apterous. Moreover, the genus *Enoicyla* is unique among the world Trichoptera in possessing these characteristics. *E. pusilla* appears to have an erratic and discontinuous distribution in Europe, and there are two other species, *E. reichenbachi* Kolenati and *E. costae* McLachlan, not so far found in the British Isles. Döhler has given an account of the genus and reviewed the literature.



Figs. 4–9.—*Enoicyla pusilla* Burmeister. (4) Labrum. (5) Left mandible. (6) Pro- and mesonotum. (7) Prothoracic leg. (8) Mesothoracic leg. (9) Anal claw.

I am indebted to Dr. G. Ulmer and to Dr. Walter Döhler for much help.

Larva (fig. 1) : to the naked eye an apparently typical Limnephilid larva ; up to 7·0 mm. in length and 1·1 mm. in width : head and pronotum chestnut-brown, legs light yellowish-brown, rest of body greyish-white. *Case* up to 10 mm. in length and 2 mm. in width ; composed of sand grains with small pieces of vegetable debris (fragments of dead leaves), conical and arched. *Head* (figs. 2 and 3) : aboral region covered with spicules, from each of which an extremely fine hair arises ; cervical foramen encircled by a deep furrow, more apparent when head is viewed from below ; genae widely separated at the ventral suture. *Labrum* (fig. 4) with light golden-brown areas between the dark brown margins and darker central area. *Mandibles* (fig. 5) with internal brush of hair and external pair of bristles present on each. *Pronotum* (fig. 6) : spicules, similar to those on the head, present in a transverse band ; pattern of dark marks as shown in figure ; prosternal horn absent. *Legs* (figs. 7 and 8) : the continuous series of spines on ventral margin of tibiae, present in most Limnephilidae, absent. *Abdomen* : dorsal protuberance on first abdominal segment, lateral protuberances not prominent ; gills and lateral tubercles absent ; two stout spines present, each arising from a disc-like base on central surface of each abdominal segment ; anal sclerite not well defined, but numerous long stout black spines present, occurring also on the anal lobes ; anal claw (fig. 9) small, auxiliary claw absent ; black mark on basal lobe.

SUMMARY

The larva of *Enoicyla pusilla* Burm. is described and figured.

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EXPERIMENTS ON SEXUAL ISOLATION IN SPECIES OF THE *MESOPHRAGMATICA* GROUP OF *DROSOPHILA* (DIPTERA)[1]

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[Communicated by E. B. Basden, A.R.C. Unit of Animal Genetics,
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Introduction

Up to now the following six species of the *mesophragmatica* group of the genus *Drosophila* are known: *D. mesophragmatica* Duda, 1925; *D. gaucha* Jaeger and Salzano, 1953; *D. pavani* Brncic, 1957; *D. altiplanica* Brncic and Koref, 1957; *D. orkui* Brncic and Koref, 1957; and *D. viracochi* Brncic and Koref, 1957. Although most of these species are allopatric for characteristic regions in South America, in several places their distribution areas overlap. Thus, *D. viracochi*, *D. mesophragmatica* and *D. orkui* are sympatric in Peru (Cuzco): *D. mesophragmatica*, *D. altiplanica* and *D. gaucha* are all found together in Bolivia, and *D. pavani* (a typically Chilean species) and *D. gaucha* overlap in a small zone in Argentine (province of San Luis).

All these species can be considered as separate biological entities, and can be distinguished by slight morphological differences, with some, as *D. pavani* and *D. gaucha*, or *D. altiplanica* and *D. orkui*, constituting cryptic (sibling) species (Brncic and Koref, 1957*a*). In previous papers by these authors it was shown that the natural populations of these six species are reproductively isolated. There is no gene exchange between them, even in the regions where they are found together.

This fact is not new to those who are familiar with the taxonomy, genetics and evolution of the genus *Drosophila*. Patterson and Stone in their revision (1952, ch. 7) point out several cases of species which are morphologically very similar or even indistinguishable, but which nevertheless represent closed genetic systems, according to our biological concept of species (Dobzhansky, 1951; Mayr, 1942). These systematic entities are important. On the one hand, it may be possible to clarify several evolutionary problems if one is able to know the mechanisms that take part in this incipient stage of speciation, based on the lack of gene exchange. On the other hand, as has been pointed out by Dobzhansky (1951, 1956) and others, the existence of cryptic species proves that morphological differentiation does not necessarily go together with evolutionary divergence.

This lack of gene exchange between different species is the result of several types of isolating mechanisms. These are usually different for each group of species, and in general one alone is not sufficient to prevent the production of hybrids.

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[1] This work has been financed in part by grants from the Rockefeller Foundation.

The object of the experiments mentioned in this paper was to study some of the mechanisms responsible for sexual isolation between the members of the *mesophragmatica* group.

Material and Methods

The following were the stocks used: *D. mesophragmatica* from Cuzco (Peru) and La Paz (Bolivia); *D. gaucha* from Rio Grande do Sul (Brazil), Sao Paulo (Brazil) and Cordoba (Argentine); *D. pavani* from Copiapo (Chile), Vellenar (Chile), Santiago (Chile) and Mendoza (Argentine); *D. altiplanica* from La Paz (Bolivia); *D. orkui* from Cuzco (Peru) and *D. viracochi* from Machu Pichu (Peru).

The single choice mating method (*i.e.* one species of male with one species of female) was used to investigate the different sexual isolating mechanisms between the species of the *mesophragmatica* group. The morphological features, the chromosomes and the phylogenetic relationships of these six species have already been analysed in previous papers of Brncic and Koref (1957*a*, 1957*b*). One or several one- to two-week-old virgin females from the above-mentioned stocks were placed in separate vials with an equal number of males of either the same or of a different species. After a delay of about four weeks, due to the slow development of the flies, the females were dissected for the detection of sperm in their ventral receptacles and spermathecae.

All matings were done in 10 × 3 cm. vials with the usual *Drosophila* food medium, and during the course of the experiment were maintained at a mean temperature of 18° C.

Results

The results of the 36 crosses studied are summarised in Table I. As no appreciable differences could be seen between the different stocks of each species, their data have been combined.

Progeny were obtained in all six intraspecific crosses, but only in six of the 30 possible interspecific ones. The heterogamic matings which were most successful were those between *D. gaucha* and *D. pavani*, where an abundant adult F_1 was obtained. These results are analysed farther on.

In the crosses *D. altiplanica* ♀ × *D. orkui* ♂,[1] as well as in the reciprocal ones, a few F_1 flies emerged. The hybrid males had atrophied testes and were totally sterile. Only a few of the females, in spite of having apparently normal ovaries, gave any progeny when back-crossed to either *D. altiplanica* or *D. orkui* males.

In the crosses *D. mesophragmatica* ♀ × *D. pavani* or *D. gaucha* ♂ the few hybrids obtained developed only up to the pupal stage.

It is interesting that in those crosses in which no progeny were obtained. the females had only non-motile sperm in their genital tract. The percentage of females with non-motile sperm indicated in Table I is only approximate, as under this column several different situations have been included, from those with abundant sperm, easy to diagnose under the microscope, to those females

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[1] The usual zoological practice is to consider the sexes in the order male-female, not female-male; and on hybrids the International Code of Zoological Nomenclature has a definite ruling (Article 18), "The notation of hybrids may be given in several ways; in all cases the name of the male parent precedes that of the female parent, with or without the sexual signs". Most Drosophilists, however, through following A. H. Sturtevant (1921, *Genetics* 5 (5) : 488-500), Th. Dobzhansky, and the Texas School have habitually placed the female parent before the male parent. The new Zoological Code may amend the present ruling (*v.* 1957, *Bull. zool. Nomen.* **14** : 122).—E. B. B.

TABLE I.—*The production of hybrids in various crosses between members of the* mesophragmatica *group of* Drosophila

Males	Females	Females dissected	Large amount of motile sperm (%)	Small amount of motile sperm (%)	Non-motile sperm (%)	Absence of sperm (%)	Hybids produced
mesoph.	*mesoph.*	100	77·00	10·00	9·00	4·00	Fertile ♂♂, ♀♀
	altipl.	34	.	.	85·29	14·7	None.
	gaucha	110	.	.	75·45	24·54	,,
	orkui	52	.	.	100·00	.	,,
	pavani	87	.	.	63·21	36·78	,,
	viraco.	84	.	.	65·47	34·52	,,
altipl.	*altipl.*	100	82·00	10·00	5·00	3·00	Fertile ♂♂, ♀♀
	gaucha	37	.	.	89·18	10·81	None.
	mesoph.	60	.	.	93·33	6·66	,,
	orkui	62	6·45	22·58	64·51	6·45	Few sterile ♂♂, ♀♀*
	pavani	58	.	.	62·09	37·93	None.
	viraco.	29	.	.	55·17	44·82	,,
gaucha	*gaucha*	100	80·00	3·00	12·00	5·00	Fertile ♂♂, ♀♀
	altipl.	32	.	.	93·75	6·25	None.
	mesoph.	88	.	2·27	78·40	19·31	Only few pupae.
	orkui	46	.	.	93·47	6·52	None.
	pavani	120	82·50	12·50	1·66	3·33	Mostly sterile ♂♂, ♀♀
	viraco.	38	.	.	57·89	42·10	None.
orkui	*orkui*	82	84·14	12·19	2·43	1·22	Fertile ♂♂, ♀♀
	altipl.	51	13·72	3·92	78·43	3·92	Few sterile ♂♂, ♀♀*
	gaucha	47	.	.	72·34	27·65	None.
	mesoph.	59	. .	.	59·32	40·67	,,
	pavani	52	.	.	69·23	30·76	,,
	viraco.	68	.	.	67·64	32·35	,,
pavani	*pavani*	104	73·07	2·88	23·07	0·96	Fertile ♂♂, ♀♀
	altipl.	35	.	.	45·71	54·28	None.
	gaucha	109	76·14	14·67	5·50	3·66	Sterile ♂♂, ♀♀
	mesoph.	53	.	1·88	81·13	16·98	A few pupae.
	orkui	45	.	.	80·00	20·00	None.
	viraco.	42	.	.	50·00	50·00	,,
viracochi	*viraco.*	100	76·00	.	22·00	2·00	Fertile ♂♂, ♀♀
	altipl.	18	.	.	50·00	50·00	None.
	gaucha	90	.	.	77·77	22·22	,,
	mesoph.	54	.	.	64·81	35·18	,,
	orkui	28	.	.	25·00	75·00	,,
	pavani	99	.	.	63·63	36·36	,,

* Some ♀♀ later found to be fertile to either parent male.

which had only very few sperm. The latter cases were most frequent, and there may be quite a range of error due to individual subjective appreciation. Nevertheless, it is clear that there is copulation with insemination between all members of the six species, and in those cases in which no progeny is obtained, the heterologous sperm are speedily inactivated within the reproductive tract of the female. The results seem similar to some cases recorded by Patterson (1954) in crosses between members of the *virilis* group. The insemination reaction (Patterson and Stone, 1952, ch. 8), frequent in other *Drosophila* species-groups, was not seen in the *mesophragmatica* complex.

In the crosses from which hybrids were obtained, a certain number of the parent females showed motile sperm in their ventral receptacle. The percentage of females inseminated, as well as the number of motile sperm found, seem to be in direct relation to the abundance and viability of the progeny observed. Only in *D. pavani* and *D. gaucha* was the number of inseminated females greater in the heterogamic than in the homogamic matings.

As both hybrid males and females from the crosses between the sibling species *D. gaucha* and *D. pavani* showed apparently normal gonads, the fertility of the progeny was tested. The F_1 sexually mature females were mated individually, or in small mass cultures, to an equal number of F_1 males. In the case of the mass cultures in which larvae could be seen, the females were placed separately in individual vials. The same procedure was used for the back-crosses. Table II summarises some of the results obtained.

TABLE II.—*Hybrids between* D. gaucha *and* D. pavani

			♀ F_1 Back-crosses		♂ F_1 Back-crosses	
Crosses	P × P	$F_1 \times F_1$	With ♂ *gaucha*	With ♂ *pavani*	With ♀ *gaucha*	With ♀ *pavani*
gaucha ♀ × *pavani* ♂						
Number of crosses .	50	318	33	36	30	30
Percentage with progeny	76·00	0	0	0	0	0
pavani ♀ × *gaucha* ♂						
Number of crosses .	88	110	37	31	30	32
Percentage with progeny	79·54	3·63	24·32	0	20·00	9·37

The first fact is that both male and female hybrids from *gaucha* ♀ × *pavani* ♂ crosses are completely sterile, not only when mated to each other but also when back-crossed to either parent. On the other hand, some male and female progeny from the reciprocal cross, *pavani* ♀ × *gaucha* ♂, are fertile, a few individuals being obtained from the back-crosses (except with *pavani* ♂) and from the crosses between them. It is interesting that only non-motile or no sperm are ever found in the reproductive tract of the hybrid females from *D. gaucha* ♀ × *D. pavani* ♂, whereas in females coming from the reciprocal cross a certain number of live sperm was observed.

These contrasting results cannot be explained only by chromosomal differences, as the hybrid females from both reciprocal crosses have the same number of chromosomes from *D. pavani* and from *D. gaucha*. This suggests the existence of some cytoplasmic or maternal influence in the sexual isolation between these two species, as has already been found in other members of the genus *Drosophila* (*cf.* Patterson and Stone, 1952, ch. 10).

DISCUSSION

As has been pointed out by Dobzhansky (1951) and by Patterson and Stone (1952, ch. 7), there are several isolating mechanisms in the genus *Drosophila*. Some of these, such as geographic, ecological or seasonal isolation, can only be discovered by a deep study of the dynamics of the natural populations, while others, such as reproductive isolation, may be investigated in the laboratory. According to the above authors, the reproductive isolating mechanisms, which can be studied experimentally, may be classified as follows: (1) mechanical isolation due to differences in genitalia; (2) sexual or psychological isolation or failure to mate; (3) insemination reaction and perhaps failure to inseminate females sufficiently; (4) death or sterilisation of cross-mated individuals; (5) gamete mortality; (6) zygote or hybrid mortality; and (7) zygote or hybrid sterility.

In the *mesophragmatica* group it seems clear that some of the mechanisms (3)–(7) play an important part in preventing genetic exchange between the species. In all crosses, except in those between *D. gaucha* and *D. pavani*, lack of sufficient insemination and gamete mortality were found, due to the small amount of sperm, of which little if any was motile in the genital tract of the females.

Moreover, in the crosses *D. mesophragmatica* ♀ × *D. gaucha* or *D. pavani* ♂, there was an early death of the zygotes, as the hybrids developed only up to the pupal stage. The zygote mortality may be due to several causes, all related to a genetic incompatibility. The cytological study of the giant chromosomes of hybrid larvae (Brncic and Koref, 1957*b*) shows that the genetic arrangement along the chromosome of one species differs from that of the other species by many inverted zones, and regions in which there is lack of coupling.

In the crosses between *D. orkui* and *D. altiplanica* the above factors, and also partial hybrid sterility, have been observed. This sterility is undoubtedly based on genetic incompatibility, as the hybrid chromosomes show a great number of inversions; it also has an anatomic expression in the atrophied testes of the hybrid males. The females, on the other hand, have apparently normal gonads, but only some of them give progeny when back-crossed to either *D. orkui* or *D. altiplanica*.

Although the chromosome configuration of *D. altiplanica* places it nearer to *D. gaucha* and to *D. viracochi* (Brncic and Koref, 1957*b*), its degree of reproductive isolation brings it nearer to *D. orkui*. In nature up to now they have been found in separate regions (*orkui* in Peru and *altiplanica* in Bolivia), but they may yet be found to overlap in some zone.

The most subtle, but not the least effective, reproductive isolating mechanisms are those found between *D. gaucha* and *D. pavani*. In Table I, it is possible to see that the number of inseminated females and of those with motile sperm is even greater in the crosses between species than in the homogamic ones. On the other hand, the hybrids are less fertile, even though anatomically both male and female gonads are apparently normal. Hybrids copulate, but the sperm are inactivated, except in some matings between *D. pavani* females and *D. gaucha* males from which a few progeny are obtained (Table II). The difference in results between these and the reciprocal crosses (*D. gaucha* ♀ × *D. pavani* ♂) may indicate the presence of some cytoplasmic or maternal factor responsible for the incompatibility.

Both *D. pavani* and *D. gaucha* males, when crossed with the five other species, give very similar results (Table I). When crossed with *D. mesophragmatica* females non-viable pupae are produced. These results, together with the other factors analysed, the similar external appearance and chromosome configuration of the two species (Brncic and Koref, 1957*b*), further suggest that they are very closely related from an evolutionary standpoint, and also more related to *D. mesophragmatica*, or at least to the female of that species, than to other members of the group.

Finally, unpublished data of Brncic and Casanova indicate that there is still another element in the reproductive isolation between these two species. With the multiple choice technique, in which males of one species are placed with females of both, it is seen that the males exhibit a tendency to copulate with females of their own species. This shows the existence of a certain degree of psychological isolation. It may explain in part the absence of hybrids in nature in the regions where both species are sympatric.

From what has been discussed, it can be seen that many reproductive isolating mechanisms operate between the members of the *mesophragmatica* group, and though they are different for each of the species, their final result is to prevent gene exchange which may cause a breakdown of the genetic systems built up by each species.

Summary

By means of the single choice mating method it was shown that between the six known species of the *mesophragmatica* group of the genus *Drosophila*, *D. mesophragmatica*, *D. gaucha*, *D. pavani*, *D. altiplanica*, *D. orkui* and *D. viracochi*, there are varying degrees of reproductive isolation. Although in all crosses males and females copulate, in most heterogamic matings the sperm are rapidly inactivated within the genital tract of the females.

In both reciprocal crosses *D. altiplanica* × *D. orkui* a few males with atrophied testes and mostly sterile females with apparently normal ovaries are obtained. From the crosses *D. mesophragmatica* ♀ × *D. pavani* or *D. gaucha* ♂, the few hybrids develop only to the pupal stage. Only in matings between *D. pavani* and *D. gaucha* is an abundant F_1 obtained, most of which hybrids are sterile, except a few males and females from crosses *D. pavani* ♀ × *D. gaucha* ♂. In the reciprocal cross 100 per cent. of the hybrids are sterile. These differences suggest the intervention of certain maternal or cytoplasmic factors.

Acknowledgment

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STUDIES ON THE MALE GENITAL TUBE IN THE DERMAPTERA

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Introduction

The existence of notable variations in the morphology of efferent ducts in the earwig and the separation of the Dermaptera from the Orthopterous group of insects were suggested by Favrelle (1934). The present observations, apart from supporting this view, seek to clarify doubts expressed by workers on other orders regarding the existence of the common ejaculatory duct in Dermaptera and reveal the presence of paired and unpaired ducts side by side, especially in *Euborellia annulipes* (Lucas) and *Nala lividipes* (Dufour). The condition showing complete independence of the vasa deferentia and the ejaculatory ducts of the two sides, described by Snodgrass (1935) in *Anisolabis maritima* (Géné), was not represented in the present study. Nevertheless, the nature of the efferent duct in *E. annulipes* presents similarities to that in such orders as the Hemiptera and Coleoptera. The reduction of the left ejaculatory duct to a vestige in the Eudermapterous *Forficula auricularia* L. (Qadri, 1940) is a more advanced development in this superfamily, since in *Marava arachidis* (Yersin), which also belongs here, both the ejaculatory ducts are present in the adult, but only one of them opens to the outside. The existence of the paired genital opening in the parasitic *Hemimerus talpoides* Walker (Jordan, 1909) in spite of the single penis in the adult, seems to have no parallel among the free living members.

The present study is based on males of *E. annulipes*, *N. lividipes*, *Forcipula quadrispinosa* Dohrn, *Labidura riparia* Pallas and *M. arachidis*. The material was collected from time to time and dissections were made in 2 per cent. saline.

Morphology of the Genital Tube

The paired vasa deferentia are uniformly thin in all the species and lead into a common seminal reservoir, formed by the fusion of the terminal ampullae of these ducts. The part of the tube behind the seminal reservoir varies considerably. In *E. annulipes* and *N. lividipes* there is an anterior paired and a posterior unpaired part, these regions being structurally quite different and distinct. The unpaired region, which has a very heavy musculature, contains the two ejaculatory ducts whose walls are strongly chitinised. Both ducts open to the outside independently. The paired region is comparatively thin-walled and has no trace of chitin lining its lumen. A short distance below the seminal reservoir each branch has a distinctly swollen area associated with an accessory gland. Accessory glands of a tubular nature are also observed at the junction of the paired and unpaired regions. In *M. arachidis* as compared with *E. annulipes*, the unpaired region alone is present, the two species agreeing with each other in musculature and in the possession of the

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paired chitinised ducts. In *M. arachidis*, however, only one of these ducts opens to the outside. On the other hand in *L. riparia* and *F. quadrispinosa*, further to the loss of the paired region, the persistent unpaired region has little in common with the other forms. Not only is the musculature of this duct different, but no trace of the cuticular grooves could be observed; the duct is also comparatively very short. In *E. annulipes* and *F. quadrispinosa* a chitinised evagination is seen arising from the ninth sternite. While this structure has no connection with the genital tube in adult *E. annulipes*, it remains attached even in the adult to the short ejaculatory duct in *F. quadrispinosa*.

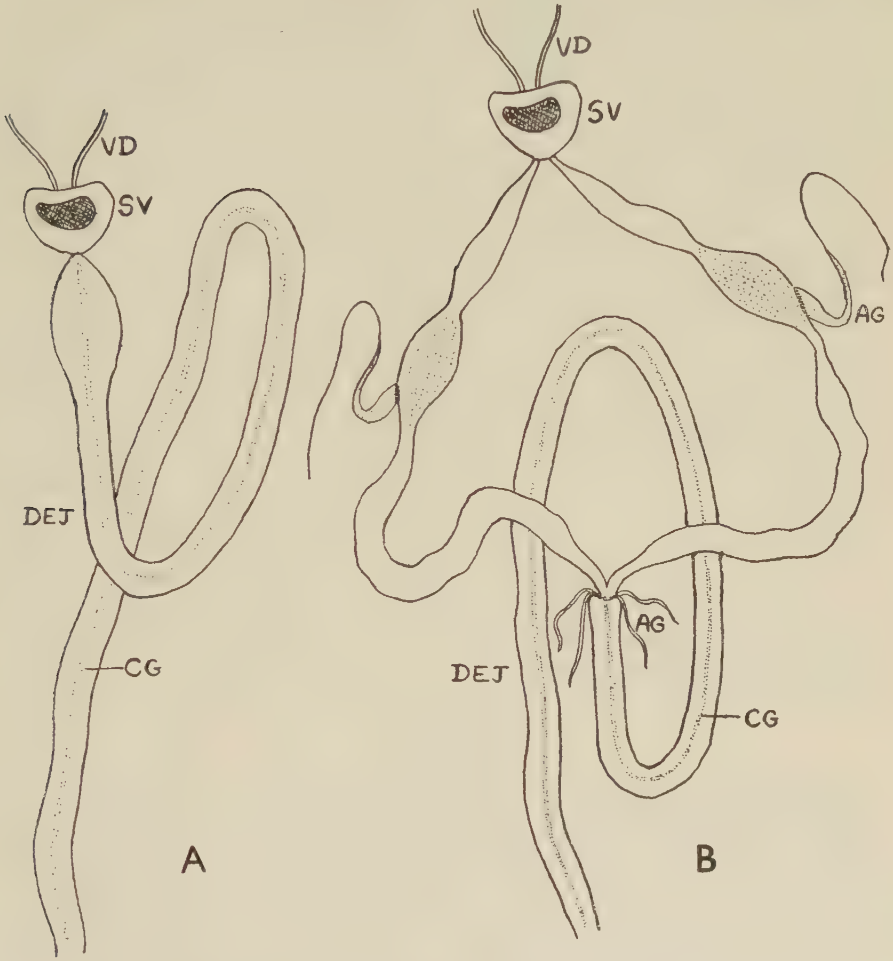

FIG. 1.—Male genital tube of (A) *M. arachidis* (Yersin), (B) *E. annulipes* (Lucas). *DEJ*, ejaculatory duct; *SV*, seminal vesicles; *AG*, accessory glands; *CG*, chitinsed grooves; *VD*, vas deferens.

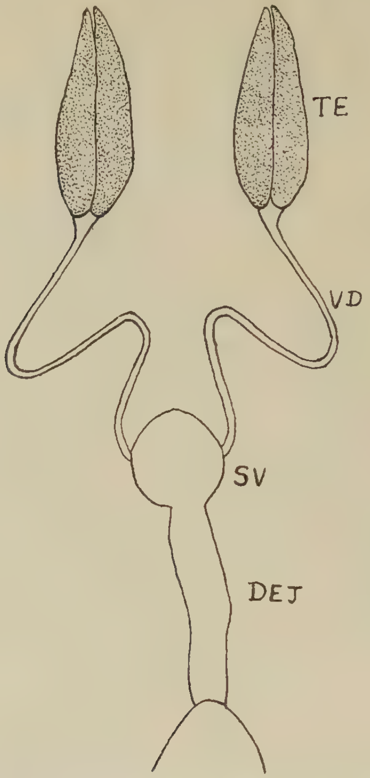

FIG. 2.—Male genital organs of *L. riparia* Pallas. *TE,* testis. (Other lettering as in fig. 1).

DISCUSSION

Studies on the male genital tube of the Hexapoda do not seem to offer sufficient explanation for the presence of paired genital pores within the alate division of this class. While, among the Apterygota, paired penes are not common in Collembola and Thysanura, the difficulty of considering the paired intromittent organs of the Protura as the homologues of such structures in the earwig has been pointed out by Snodgrass (1936), because of " the different segmental relations of the organs in the two cases ". The parallel exhibited by the mayflies in this respect is equally inexplicable. In addition the Dermaptera provide greater opportunities for tracing the evolution of the paired gonopore to its unpaired condition in the Endopterygota as well as in the higher orders of the Exopterygota itself. Within the single family Labiduridae different degrees of development of the exit tube are encountered. The bipartite type of genital duct in *A. maritima* represents the Ephemeropterous condition, and the presence of paired and unpaired regions in the exit tube in *E. annulipes* represents a condition similar to that in Homoptera and Coleoptera. The difference in structure of the paired region from its unpaired counterpart in the latter species is further indicative of the independent origin of this part, a condition not unknown in Homoptera (Pruthi, 1924).

The course of development followed by the unpaired part of the genital tube in the Eudermapterous forms helps to explain the last two stages in the evolution of the gonopore. In *M. arachidis* the retention of both the ejaculatory ducts, while only one is functional, seems to be the beginning of the degeneration of one of them. In *F. auricularia* the left ejaculatory duct is reduced to a vestige, losing its opening to the outside and thus establishing the unpaired gonopore with a single ejaculatory duct within this group.

In *Diplatys* (a primitive genus with paired intromittent organs), the virga in each penis is forked (Hincks, 1953), thus affording four external orifices to the exit tube. The suppression of one of the penis lobes, though exceptional in the Protodermaptera, occurs in members of Karschiellinae and Parisolabinae (Hincks, 1947). The single penis with two functional ejaculatory ducts in *H. talpoides* represents a condition intermediate between the Proto- and Eudermapterous types of male genital armature, with a closer resemblance to that in *M. arachidis*, where one of the ejaculatory ducts has lost its opening to the outside. It is difficult to trace the affinity of the parasitic form to either of the two superfamilies on the basis of the rest of the genital duct. Nevertheless, Rehn and Rehn (1936) do not doubt the relationship of the Hemimeridae with the Eudermaptera. If this relationship could be further emphasised by a comparison with *M. arachidis*, as stated above, then the similarity in the female reproductive system of these two species (Ramamurthi, 1956)—both showing viviparity—may be yet another point worthy of consideration.

The significance of the association of the accessory glands with the paired region of the ejaculatory duct in *E. annulipes* is noteworthy in view of their total absence in all the other forms with no paired region.

Concerning *Labidura*, Imms (1951), quoting Meinert, indicates that the ejaculatory duct in this genus is paired but the present study does not support this view. The same authority refers to this duct as a mesodermal derivative which, however, does not seem improbable considering its nature as described above.

SUMMARY

1. The variations exhibited by the ejaculatory ducts within the Dermaptera are described and discussed in detail. These illustrate the stages which may have taken place during the evolution of the gonopore from its paired to unpaired condition within the Pterygota.

2. The presence of the paired and unpaired regions in the exit duct of the efferent system in *E. annulipes*, while representing a similar condition in the more advanced orders, is also associated with the origin of the accessory glands which are noticed for the first time in this group.

3. The similarity in the female reproductive system of *M. arachidis* and *H. talpoides* is also observed in the male reproductive system, the ejaculatory ducts in the parasitic form representing a condition intermediate between the Proto- and Eudermapterous types of genital armature.

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ON THE HABIT OF *ARIXENIA ESAU* JORDAN (DERMAPTERA)

By Lord Medway.

Introduction

Arixenia esau was first described by Jordan from nymphal specimens found by the dealer Gerrard in the pouch of the Naked Bat (*Cheiromeles torquatus*), sent in spirit by Charles Hose from Sarawak (Jordan, 1909). Where the bat was collected is not mentioned but there is an extensive colony of these Dermaptera in association with large numbers of this bat in the huge Subis cave on the Niah River of IV Division Sarawak (at 113° 47′ E., 3° 48′ N.). Hose was Resident of the Baram, a district which in those days included Niah, and is known to have visited and collected in the cave, which may therefore be the type locality of *A. esau.*

Jordan entitled his original paper " Description of a new kind of apterous earwig, apparently parasitic on a bat ", but expressed several doubts to stress the " apparently ". He also ventured other opinions on the habit of the insect, now quoted below :

He was " inclined to attribute to accident the occurrence of such a large insect in the nursing pouch of the Naked Bat " (p. 313).

The mandibles of *Arixenia* appeared to him " much more suitable for brushing food into the mouth than for cutting it up " (p. 316). Yet he found, in the oesophagus, remains of apparently fresh insect food, which " if correct would justify the conclusion that *Arixenia* feeds, perhaps incidentally, also on live or freshly killed insects " (p. 313).

No other records of the species occurred until a collection was made in 1952 from a Naked Bat colony in Malaya (Cloudsley-Thompson, 1957), and, as this colony was destroyed, Niah appears to be the one remaining known locality for *Arixenia esau.* It was not, however, recorded in scientific literature, and no work could be done to test Jordan's original suggestions (*repeated later*, Burr and Jordan, 1913).

However, while working for the Sarawak Museum under the direction of the Curator, Mr. Tom Harrisson, I spent several weeks in Subis cave during 1957 and was able, incidentally, to study *Arixenia*, as far as topography allowed, and to make several simple experiments, all of which have confirmed Jordan's original suggestions. I should like to thank Mr. Harrisson, and Mr. M. W. F. Tweedie, formerly Director of the Raffles Museum, Singapore, who roused my interest in the insect, and who has been of great help in the preparation of this paper.

Arixenia esau at Niah

The host, *Cheiromeles torquatus*, is a large insectivorous bat. As its English name implies, it is virtually hairless ; the tough skin is dark brown, very loose and wrinkled, rather velvety to the touch, and densely pitted with glandular pores. In addition there is a large gland at the base of the throat, which exudes a nauseating stench if cut or prodded—as of burnt feathers and hair; the lumen of this gland is concealed by a fold of skin, which is often referred to as the "gular pouch" of the bat, about which there are several misconceptions, arising from an initial confusion of Jordan's.

Arixenia has never been found in this "pouch", and I doubt if it ever will, for there is no room for such a large insect. Jordan had presumably never seen the bat, for he failed to distinguish between the gular *fold* (a better term) and the extensive subaxillary pouches, into which the tips of the bat's wings fit when closed at rest. In the first sentence of the first paragraph of his 1909 paper, Jordan quotes Gerrard and Son, who affirm that the specimens were found in the "sack formed by the membrane of the wing of *Cheiromeles torquatus*". Midparagraph he introduces the gular pouch, and by the end he has transferred *Arixenia* into this uncomfortable nook. I have not seen any *Arixenia esau* interested in entering or feeding at this "gular pouch" on a bat, dead or alive.

The colony of these bats at Niah is far out of reach, about 250 feet overhead, high in the semidarkness of the cave roof in the centre of a very tall chamber behind the equally huge west mouth of the cave. An estimated 20,000 individuals, closely packed, roost here. Directly below them and nowhere else in the cave (which has a total floor area in plan of 26 acres) are large numbers of *Arixenia esau*, most of them gathered into four groups, each clustered at the highest point of one of the odd poles which stick up from the guano, rotten relics of the climbing equipment of birds' nest collectors. As will be described below, the insects tend naturally to climb upwards; this accounts for their presence in these sites, which are the only places where they can survive, for the bats' droppings are valued as fertiliser by the local natives, and the cave floor is swept clean every day by Niah Dayaks.[1] On these logs are *Arixenia* of every instar; adults run around freely in copulation, the female in front, the male carrying his abdomen arched over his head to clasp the slightly elevated end of the female abdomen. This posture differs from that of *A. jacobsoni*, as described by Jacobson: "Copulating couples could be seen everywhere, their heads turned opposite ways, and one of them pulling the other backwards" (Burr, 1912).

The insects have a slightly lemony smell. They are parasitised by a mite, and carry the same fleas that are found on *Cheiromeles*, which however leave the insect at once if disturbed.

In all, there are about a thousand head of *Arixenia* on the cave floor, but a large number of shed skins as well as living insects of all growth stages fall daily from the heights above, and there is evidently a far greater population among the roosting bats. All specimens so far examined have been identified as *esau*.

Twenty-two *Cheiromeles* have been collected in flight, away from the roost; no *Arixenia* of any stage were found on them, and, as the dissection of a gravid female has shown that they are ovoviviparous, there is no possibility that eggs are laid somewhere on the bat. Thirty-two *Cheiromeles* have been shot at the roost, and of these one only carried a single *Arixenia*, an adult male.

Yet there is no doubt that *Arixenia esau* feed primarily on the products of the glandular skin of the bat. They are attracted alike to dead and living

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[1] Steps have now been taken by the Sarawak Government, through the Museum, to prevent the wholesale removal of fresh guano from the cave, which has been scheduled as a National Monument.

Cheiromeles. It is a clumsy bat—returning adults often collide with the cave wall and are stunned ; and young bats also lose their grip ; both fall to the floor below the roost. *Arixenia* are always found on those dead or dying bodies, crawling over them with an excited jerky gait, exploring every fold and pouch, or grazing restlessly on the pitted skin.

Insects from the floor behave in the same way on a human hand. Clinging with their sharp curved claws, hard to shake off, they move jerkily around, with near hysterical agitation ; it is a very ticklish feeling. All ignored the skin of my palms, some found my metal watch strap an impassable barrier, and several began to feed on the soft sweaty skin between and on the back of my fingers. In feeding they pressed their mandibles to the skin, and, opening and closing them rapidly and continuously, scraped the skin surface and moved steadily forward. The direction of movement was always upwards, and changed at once if the hand was turned. The sensation was not painful, but very irritating—like the gentle beginning of a subtle torture—and since each " bite " was applied to a fresh place, would never break the skin, but would clearly scrape the surface clean.

Arixenia esau were not seen attacking each other in the cannibal manner of *A. jacobsoni* as described by Jacobson, with evident disgust (*vide* Burr, 1912). But, in Niah cave, three were once seen, among the crowd on a log, with their heads under the elytrae of a Tenebrionid beetle, feeding on it while it still lived.

These beetles have been identified by Mr. E. B. Britton of the British Museum (Natural History) as *Tenebrio antricola* Blair. The species was first described from a Javan cave, but unfortunately the author makes no specific mention of the presence or absence of *Arixenia* (Blair, 1936). At Niah there is clearly some relationship between the beetle and *Arixenia* and/or *Cheiromeles* ; it too is found only at this one spot in the cave, on the floor and on the logs frequented by *Arixenia*, and falls in numbers from the cave roof. It is more light-shy than *Arixenia*, and burrows into the guano, or pushes into cracks in the wood ; when the insects gather together, as they often do, it is found at the bottom of the pile. Jacobson also recorded " different species of Tenebrionidae " with *A. jacobsoni* in his Javan cave.

It does not seem to be parasitic on the bat, for it has none of the vigour or grip of the agile Dermapteran, and falls off at the first shake ; it shows no particular interest in bats except as hiding places from the light. The slight experiment detailed below shows that it will eat fresh insect food.

Chitinous remains were found in the alimentary canals of specimens collected from the cave floor, but it is not clear whether these are of fresh insect food or from the excrement of the Naked Bat.

EXPERIMENTS AT NIAH

(1) *Arixenia* and a dead bat, *Cheiromeles*

A group of five *Arixenia* collected from the cave floor were put in one corner of an open aluminium box 1 foot 6 inches by 2 feet, and a freshly killed bat was dragged over the bottom and left in the corner diagonally opposite. The insects at first huddled together, or tried to climb the side, but gradually began to wander. After three minutes an adult female found the trail of the bat and followed it excitedly, stopping only a moment at a blood smear, but within 4 inches of the bat she turned aside, and returned to the group. After eight minutes a nymph found the bat, at once crawled on to it and began to clamber excitedly over the corpse, probing into every fold, but showing no attraction towards the gular gland, and only entering the wing pouch briefly in an exploratory manner.

A number of *Arixenia* from the cave floor, shaken on to the dead bat, all behaved in the same way; they ultimately calmed, and settled down to feed on the skin of the bat in the manner already described, their heads down, tails raised, mandibles working steadily.

On one occasion one male and one female made repeated visits to the vagina of a dead bat, lapping up a white fluid that had extruded, and, when this fluid had gone, thrusting their heads into the vagina for periods of 20–62 seconds. However, no other *Arixenia* showed interest in this fluid on dead or living bats. No attention was paid to the sexual organs of males, to the anus of either sex, nor to clotted blood.

(2) *Arixenia* on a living bat

When a second bat, a female alive and active, was placed beside the dead one, *Arixenia* soon crawled on to it from the latter. Again they moved rapidly in their excited manner, which obviously irritated the bat considerably, and it used its hind feet, forearm and clawed thumb to fling them off. As a result, the only safe place for the insects to settle was over the hindquarters of the bat, and here they congregated, feeding head upwards as already described. After doing so for half an hour, a female crawled upwards off the bat (which was hanging from a bench) and hid under papers on the bench. It was put back, but each time, instead of roaming excitedly, it crawled up at once, straight off the bat.

On dissection, the crop of this insect, and of others after a day feeding on the bat, proved to be filled by a dark fluid. Examined under a hand lens, this was seen to consist of many small particles in suspension, without any recognisable structures. The very full gut of the one male *Arixenia* found on *Cheiromeles* shot at the roosting site was preserved in spirit and brought to Kuching for microscopic study. The contents had coagulated, but contained no recognisable material.

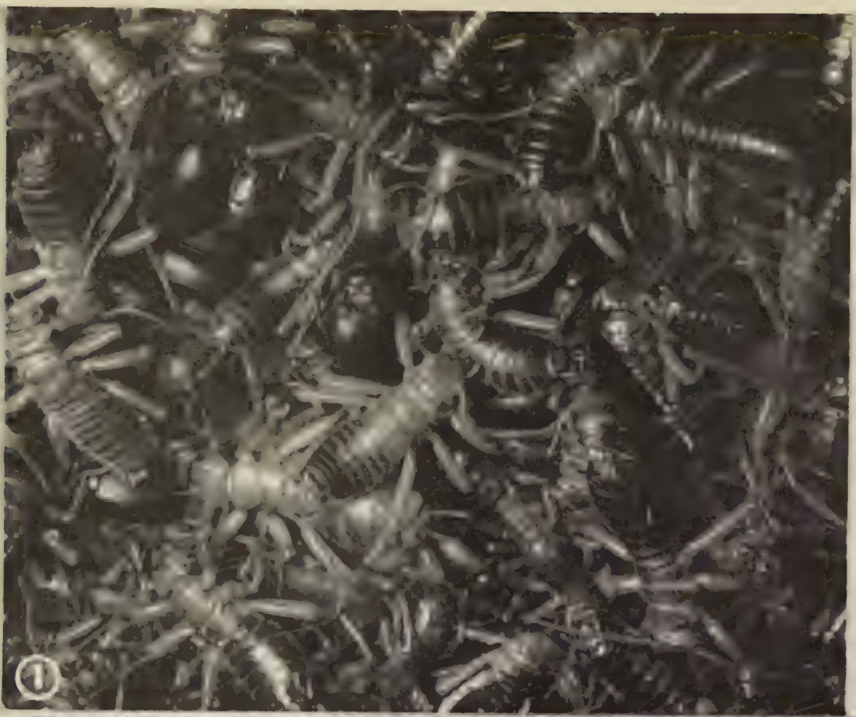
In no case did any *Arixenia* attempt to feed at the gular gland.

(3) *Arixenia* and other food

After four days starvation, adults and nymphs showed no interest in the following foods: butter, sugar, cooked rice, salt fish, corned beef. They did not attack each other, but at once set upon crushed or injured insects of whatever species, including their own.

(4) *Arixenia* and *Tenebrio antricola* Blair

Five *Arixenia* of different growth stages and five specimens of *Tenebrio antricola* were shut up together for four days in a small box. All survived unharmed, but when one of each was crushed and reintroduced to the box,



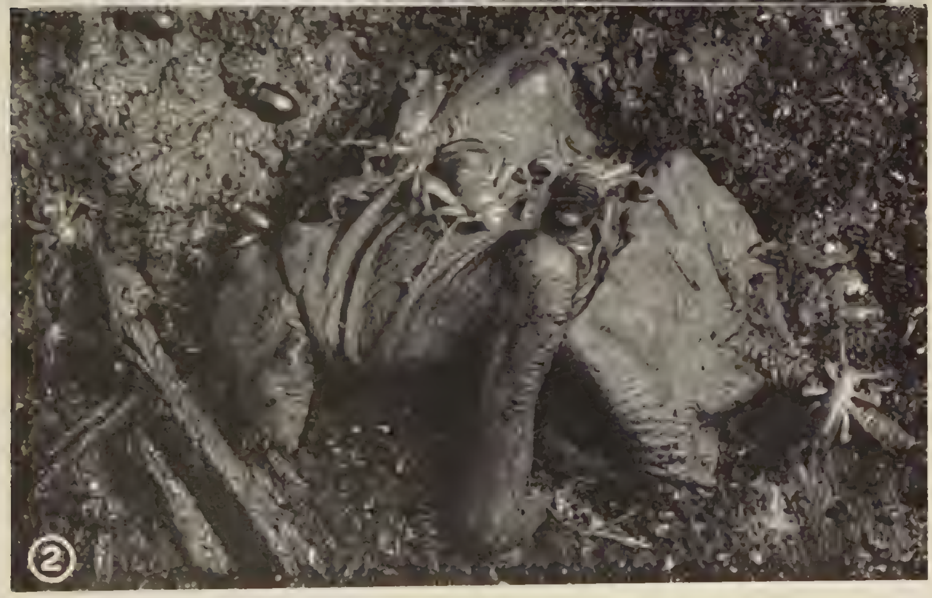


FIG. 1.—*Arixenia esau* Jordan and *Tenebrio antricola* Blair on a wooden pole; Niah Cave. iii.1957.

FIG. 2.—*Arixenia esau* on a dead bat, *Cheiromeles torquatus*; Niah Cave, iii.1957.

(Photographed by M. W. F. Tweedie.)

both insects set upon the bodies—each after its own manner, *Arixenia* voracious and hysterical, squabbling, dashing around with a leg or other fragment in their jaws, *Tenebrio* placid and persistent.

CONCLUSIONS

From these observations and simple field experiments, it appears that *Arixenia esau* is parasitic on *Cheiromeles torquatus*, insofar as its principal diet is some product of the glandular skin of that bat. It is likely, however, that it only goes on to the host to feed, and, when satisfied, crawls upwards again to the rock wall of the cave roost, where most of its time is spent. But if hungry it will eat dead or injured insects, including its own species. The part of *Tenebrio antricola* in this relationship is not clear.

SUMMARY

1. The presence of a colony of *Arixenia esau* Jordan in Subis cave at Niah, in Sarawak, is recorded.

2. Observations and simple field experiments made on the insects of this colony during November, 1957 are described.

3. A parasitic relationship between *Arixenia esau* and the Naked Bat, *Cheiromeles torquatus*, is clearly indicated ; the former are shown to feed on the epidermal products of the latter.

4. *Arixenia esau* is also shown to attack and eat injured insects (including its own species) when hungry.

5. A further relationship between *Arixenia esau* and/or *Cheiromeles torquatus* and a beetle, *Tenebrio antricola* Blair, is also indicated, but is not made sufficiently clear by present observations.

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ELYTRAL CHARACTERS AND SEXUAL DIMORPHISM IN A SURREY POPULATION OF *AGABUS MELANARIUS* AUBÉ (COLEOPTERA : DYTISCIDAE)

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[Communicated by J. Balfour-Browne]

In June, 1952, the late Lt.-Col. C. J. F. Bensley showed me a small body of water in S.W. Surrey near Haslemere, where he had found an abundance of black Dytiscids. A sample of 30 specimens from this and two neighbouring pools consisted entirely of *Agabus melanarius* Aubé, for which Balfour-Browne (1950 : 140) gives the nearest locality as Haldon Moor, South Devon.

My purpose in what follows is two-fold : (*a*) to help the student more effectively to make use of the diagnostic elytral characters since this species, of which the known localities are few and widely dispersed, is easily overlooked because of its resemblance at first sight to other commoner members of its genus, such as *bipustulatus* L.; (*b*) to draw attention to the sexual dimorphism of the elytral sculpture, especially that due to the strong longitudinal elongation of many major meshes of the elytral reticulation in a considerable proportion of the female sex.

I am indebted to Professor F. Balfour-Browne for checking my determination of the species, to Mr. J. Balfour-Browne for valuable advice and permission to work in the Coleoptera Department of the British Museum (Natural History) and to Miss D. J. Jackson for constructive criticism. Mr. D. E. Davies of the Anti-Locust Research Centre and Mr. A. M. Walker of the Oxford University Unit of Biometry have helped me with statistical matters. I much appreciate the assistance kindly given to me by all these extremely busy scientists.

The characteristics of the habitat agree in general with those reported by collectors elsewhere (Balfour-Browne, *ibid.*). The colony continues to survive and is being studied ecologically.

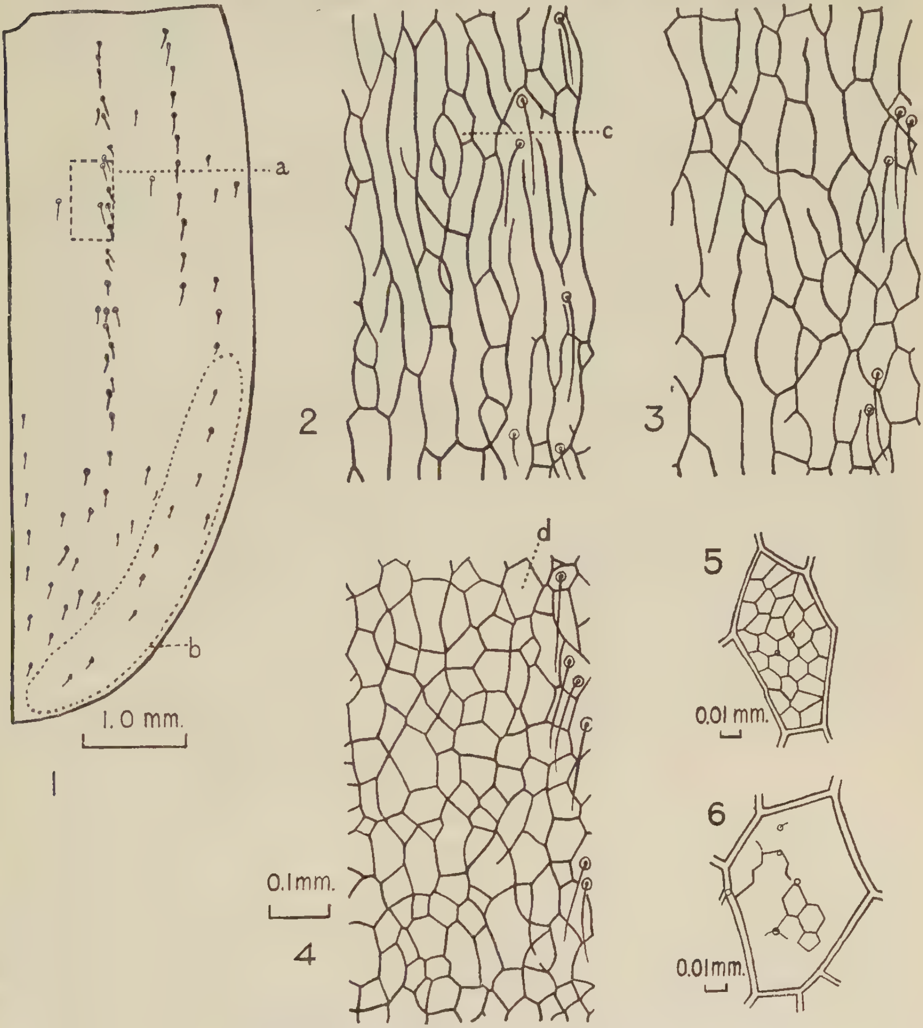
It has been found that the species may readily be recognised in the field if one elytron of a living specimen is lifted and examined from below. The deep black colour and contrasting pale submarginal band (fig. 1*b*) in the distal half are more distinct than in any other British *Agabi*. The only species resembling it in this way is *A. didymus* Ol., which is easily distinguished by the geminate pale spots. The elytra of our other black *Agabi*, when thus viewed, appear light brown.

Many living specimens have been so examined without injury. Left to itself in water containing weeds affording a foot-hold, the insect restores the elytron to its normal position.

The elytral reticulation seen through a hand-lens (× 10) and considered with colour, shape and body size, is generally diagnostic. It does, however, vary widely and the method of identification given above serves as a useful check in doubtful cases.

The variation of the reticulation was studied with some precision by means of transparent impressions.

Technique.—A solution of gum arabic in water, saturated at about 15° C.,[1] when painted thickly over an elytron, allowed to dry and removed with fine-pointed forceps, produces a transparent film. The film displays a distinct



FIGS. 1–6.—*Agabus melanarius* Aubé. (1) External view of elytron as seen *in situ*; *a* = reference area, *b* = pale stripe. (2) Major reticulation of a female (No. 1) showing maximal mesh elongation. (3) Major reticulation of a male (No. 11) showing maximal mesh elongation. (4) Major reticulation of a male with minimal mesh elongation. (5) Detail of mesh *c* of figure 2. (6) Detail of mesh *d* of figure 4. Figures 2–4 are to the same scale and represent the area *a* situated as in figure 1. On the specimen this area is 0·76 × 0·39 mm. It lies 1·28 mm. posterior to the scutellum apex and 0·61 mm. from the suture.

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[1] Small crystals of thymol are added to check fungi.

impression of both macro- and microscopic details. It generally separates from the elytron as it dries.

This, mounted dry on a slide under a cover-slip ringed with balsa cement, gives a clear image when focused with a microprojector[2] on a white surface. This image may be easily traced. One or more cracks tend to form in the film when it is flattened on the slide but these are generally no serious handicap. Figures 2–6 were prepared in this way. A subsequent check by direct microscopic examination of the elytron is made to discriminate between dust particles and the impressions of the surface structure. Figure 1 was drawn with the aid of a camera lucida direct from the specimen.

A rectangular reference area, placed as in figure 1*a*, was selected and all reticulation to be analysed was taken from this region. A rectangle of the chosen proportions, at the required magnification, was drawn in red on a large card together with the line of the suture and the apex of the scutellum in their correct relative positions. The card was placed on the screen so that the appropriate part of the image occupied the rectangle and the required measurements and counts could then be made.

Sexual dimorphism.—For purposes of this paper, only major meshes at least four times as long as wide are called "strongly elongated". Meshes partly within the reference area are counted as in it. It has been found possible with a random sample of 48 (24 of each sex), collected between 1952 and 1955, to divide the specimens into two arbitrary groups. Group A is defined as those having, in the reference area, at least five strongly elongated major meshes (figs. 2 and 3) and Group B as those with less than five (fig. 4). There is no evidence of statistical heterogeneity with regard to the portions of the sample collected in 1952–53 and 1954–55.

Table I analyses the frequencies with which the members of the groups occurred in each sex.

TABLE I.—*Association of strong mesh elongation with sex*

	Frequencies of specimens having, within the reference area and strongly elongated—	
	> 4 meshes, Group A	< 5 meshes, Group B
Males . .	1 (No. 11 of Table II)	23
Females .	10 (Nos. 1–10 of Table II)	14

The data suggest a partial sexual dimorphism shown by an association of strong mesh elongation with femaleness.

The probability of this frequency distribution, calculated by the exact method (Yates, 1934 : 219), is 0·0022. Thus the partial sexual dimorphism may reasonably be regarded as a reality—over a third of the females having a degree of mesh elongation possessed by few males.

That most of the females of Group A are far from border-line cases is shown by Table II.

Body length to the nearest 0·5 mm., with the head in the usual bent down position, varies from 8·5 to 9·5 mm. in both sexes.

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[2] The projection beam is passed through 4·5 cm. of pure glycerol in a cooling-trough. The film may otherwise be badly warped.

TABLE II.—*Frequencies of strongly elongated meshes in the reference area*

	Index No. of specimen										
	1	2	3	4	5	6	7	8	9	10	11
Number of meshes* of $L/B > 4$.	12	10	9	9	8	8	7	7	6	6	6
,, ,, ,, ,, $L/B > 5$.	7	5	7	3	6	2	5	3	3	0	2

L/B = length/breadth.

* Including those in the next line.

To obtain an accurate index of elytron length, the distance from scutellum apex to elytron tip was measured to the nearest 0·1 mm., with an eye-piece micrometer. In random samples of 15 of each sex, this varied from 6·2 to 7·0 mm. for the males and from 6·2 to 6·9 mm. for the females. The male mean value 6·63 mm. was non-significantly greater than the female mean value 6·57 mm. ($t =$ 0·620 ; $P >$ 50 per cent.). The respective standard deviations of the means were 0·263 and 0·205.

No relationship was found between mesh elongation and elytron length in the female sex. Spearman's coefficient of rank correlation for 12 specimens was — 0·16. Mesh elongation is not therefore due to allometric growth.

The micro- or primitive reticulation (Balfour-Browne, 1940 : 29 and 1950 :12), in and near the reference area, shows total sexual dimorphism. That of the females, in all but the very small major meshes, is generally complete or nearly so (fig. 5) and marked by distinct grooves. In the males, that which is marked with at least equal distinctness is far from complete, occupying, unlike that in any of the females, less than half the combined area of the major meshes enclosing it (fig. 6).

In the male sex, however, in addition to the very incomplete but distinct micro-reticulation, there is, just discernible even on the gum impressions, an extremely faint indication of further micro-reticulation which usually nearly fills the enveloping major mesh.

SUMMARY

(1) *Agabus melanarius* Aubé is recorded for the first time in South-East England.

(2) A simple method of recognising specimens in the field is given.

(3) A technique of drawing and measuring elytral sculpture by using transparent impressions is described.

(4) A wide range of variation (unrelated to elytron length) in the degree of elongation of the major elytral reticulation in the discal region is reported.

(5) It has been found that the sexes differ significantly in the range of variation of both major and micro-reticulation—there being a large overlap in the former but none in the latter.

POSTSCRIPT

It seems unlikely that this Surrey population is entirely unique with regard to the variation of the major elytral reticulation. Small numbers of specimens of *A. melanarius* from other British localities have been examined in the Hope

Department of the Oxford University Museum by kind permission of Professor G. C. Varley, and from the Continent in the British Museum. These showed similar variation and included Group A females. The reticulation pattern of specimen 1 (fig. 2) was not, however, paralleled by that of any specimen from outside Surrey, but this may only be because of the comparative smallness of the samples. The reticulation pattern of specimen 1 closely approaches that of both sexes of *A. striolatus* Gyllenhal.

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Book Notices.

The Principles of Biological Control. By H. L. Sweetman. 4to. Dubuque, Iowa (W. C. Brown), 1958. Pp. xii, 560: text illust. $8.75.

This work is a revised and extended version of *The Biological Control of Insects*, published in 1936. It had its inception in the courses given by the author to students at Massachusetts State College, and the text is designed to serve undergraduate and graduate students and research workers with interests in the biological control field.

The purpose of the work is to acquaint the reader with life histories, habits, methods of handling and utilization of the organisms which are being used for the control of insect and other pests; and the subject matter is so arranged that selected portions can be offered to students without breaking the continuity of the whole.

The volume is divided into 15 sections and there are chapters on the theoretical basis of biological control; the use of resistant hosts; micro-organisms and biological control (antibiotics; bacterial, fungus, virus and protozoan diseases); parasitic and predatory vertebrate and invertebrate animals; biological relations of beneficial insects to their hosts and prey; handling of beneficial insects and the biological control of pest plants.

A survey and analysis of world literature has been made in the preparation of the text and there is an extensive bibliography arranged by chapters. There are also numerous photographs and line drawings.

The Lepidoptera of Formby. By M. J. Leech and H. N. Michaelis. 8vo. Raven Entomological and Natural History Society, 1958. Pp. 38, text illust. 2*s*. 6*d*.

This work is dedicated to the memory of the late G. de C. Fraser, founder of the Raven Society.

It is based on his lists of the Lepidoptera of Formby, 1946 and 1947, and additional records published in the reports of the Society for 1946–51, which have been brought up to date by M. J. Leech by the inclusion of recent material. H. N. Michaelis has contributed a list of the smaller moths, and the new work now contains the names of some 700 species of Lepidoptera.

The foreword by the Hon. Secretary of the Society describes the physical features of the Formby district, which has long been recognised as an excellent collecting ground by Lancashire entomologists. A bibliographical notice of G. de C. Fraser is also included.

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